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The Subspecies Concept and Its Taxonomic Application

E. O. WILSON and W. L. BROWN, JR.

ELEVEN years ago, Mayr summed up and co-ordinated in his *Systematics and the Origin of Species* the taxonomic principles and methods that had gradually come to be recognized as basic and practical by many of the specialists working with the better-known groups of animals. Founded in the genetical precepts of neo-Darwinian evolutionary theory, Mayr's synthesis dealt most importantly with the nature of the species, which he held to be an objective and definable phenomenon, and with the geographical variation shown by populations composing the species. His species criterion was the occurrence in nature of free interbreeding, actual or potential, between members of a population or between populations; different species, he believed, are those populations possessing any factors intrinsic to their member individuals that will act to prevent interbreeding *between* the populations of a degree as free as that *within* each population. The basic reasonableness and operational advantages of Mayr's criterion struck an immediate wide and favorable response among many segments of taxonomic opinion, and his principle has been applied with considerable enthusiasm and with generally improved results to many and varied groups of Recent, sexually reproducing animals.

Along with widespread approval, this version of "population systematics" has aroused some outright opposition, as well as some more tempered criticism of particular phases of Mayr's argument. The outright opposition comes largely from those who either have not read carefully enough the various expositions of population systematics, starting with Mayr's, or who for some reason have failed to understand what we regard as for the most part a clear and simple thesis. Most of those so opposed, like M. W. de Laubenfels (1953) and Ruggles Gates (1951), insist upon regarding Mayr as having postulated that species are basically separated by *sterility barriers*. Starting with this thoroughly mistaken notion, de Laubenfels, Gates, and their school find it easy to bowl over straw men in all directions. De Laubenfels, for instance, is horrified to note that "Some dictionaries, many lesser zoologists, and the one whom many consider to be the greatest living systematist, propose a criterion of complete genetic isolation for species determination. Already they propose that most kinds of wild ducks are all one species. . . . Even many wood warblers are all one species [References?] . . . . By the geneticist's definition tigers are at best a subspecies of the lion, and bison merely a race of domestic cattle." The case of the lion and the tiger especially is so often used in this connection that we feel it would not be superfluous to make an example of it by pointing out the characteristics that prove these two forms species: (1) the breeding ranges of the lion and tiger overlap broadly in southern Asia, and the two species have occurred, at least in the recent historic past, in closely contiguous territories in India; (2) there is no sign that the Indian lion has been genetically affected through interbreeding with the surrounding tiger populations, or vice versa; (3) our principal reference (Burton, 1933) offers no evidence for any hybridization between lions and tigers in nature; (4) differences in breeding behavior, for instance, while not very well studied, seem nevertheless to be of a kind

that may well act to prevent genetic interchange between the two species; (5) hybridization, even if it did occur, would not justify reducing the two species to races unless it could be demonstrated to be free and introgressive at the zones of actual contact.

Of course, Mayr, Dobzhansky, Stebbins, and many others have repeatedly observed that hybrid sterility is only one of several possible intrinsic mechanisms that can prevent two populations from interbreeding effectively. In the place of *intrinsic failure to interbreed freely in nature*, which is Mayr's criterion, de Laubenfels and Gates somehow mistakenly and persistently substitute *cross-sterility*. Once the nature of this misinterpretation is fully realized, there is little excuse left for accepting criticism of population systematics aimed in this direction.

Criticism of a more useful sort comes from other sources. First may be mentioned the objections of the paleontologists (latest reference: Simpson, 1952). These workers place emphasis upon the difficulties arising when population systematics is applied to species-evolution as it occurs through geological time. Obviously, species do arise from units that are not distinct as species, so that the intermediate time stages, however brief, destroy the sharpness of the species criterion. More important is the apparent fact that species populations may evolve new characters in time without undergoing any splitting; for instance, one finds a population represented in each of several successive strata by what appear to be slightly and progressively differing species that can only be taken as cross-sections of a continuum. This criticism does not destroy the basis of population systematics, but it leads us to re-emphasize an important qualification that must be made: *species distinctions hold only for the consideration of a single time-transect.*

A greater difficulty is expressed in the disagreement of some observers concerning the interpretations to be placed upon allopatric populations (i.e., populations with geographically separate breeding ranges) that are not very obviously distinct as species. Most authors rely on taxonomic judgement in treating such populations, but some have tried to apply a rule whereby allopatry uniformly marks either all species or all subspecies. The situation with regard to sympatric versus allopatric populations deserves careful attention for the following reasons. If two populations have separate geographical ranges, there may exist between them any degree of interbreeding potential from full to none at all. Thus, theoretically and probably in fact, allopatric populations may show every degree of divergence up to that of full species, and will in this sense blur the fine distinction that characterizes the species as a category. If, however, two allopatric populations extend their ranges unto geographical contiguity, or otherwise become sympatric, their interbreeding reaction theoretically can be expected to establish very quickly whether or not they have diverged to the species level. If they interbreed freely and produce a hybrid population that is in no way reproductively or selectively inferior to the parent populations, then they are clearly to be regarded as conspecific. If they do not interbreed, or if their hybrids are relatively rare and sporadic or otherwise show a reduced ability to form a self-maintaining population as compared with the parent populations, then the latter must be counted as separate species.

Different populations newly arrived at sympatry after having reached an intermediate degree of loss of interbreeding potential will probably go quickly and unequivocally to either the species or subspecies level: any partial intrinsic barriers will be strongly selected either for or against because of the simple fact that it is disadvantageous for the parental populations to maintain the mass production of inferior or sterile hybrids. There is some evidence that this selective process may be among the most important mechanisms involved in species formation (Dobzhansky, 1952, p. 208). Consequently,

sympatry is more than an observer's criterion for deciding whether two populations are distinct as species; in any given case it may have been the final and essential factor that actually forced the species separation.

Since no such mechanism is operative in the differentiation of allopatric populations, there will be no clear-cut lower delimitation of species. *These populations must be dealt with arbitrarily* by gauging the genetic divergence through observed characters—morphological, physiological, and behavioral—according to standards based on comparison with the observed divergence of related sympatric species populations.

Therefore, Mayr's interbreeding criterion for the species, if qualified by the restriction of absolutely definable units to a single time-transect and to sympatric situations (the "non-dimensional species"; Mayr, 1949), and extended arbitrarily but with obvious justification through the analogy of character divergence to allopatric populations, seems to provide a natural, consistent, and practicable baseline for systematic theory.

Geographical Variation: The Subspecies Concept

Along with his analysis of the nature of the species, Mayr (1942) gave an extensive review of the evidence on variation within the species. He was mainly concerned with variation of populations as correlated with geography, and particularly with the properties and evolutionary significance of the subspecies, a category generally regarded as synonymous with the geographical race. The subspecies were conceived of as genetically distinct, geographically separate populations belonging to the same species and therefore interbreeding freely at the zones of contact. Many populations previously considered species were found to fit these conditions and were combined as subspecies in a single polytypic species. Mayr also extended the racial category to include closely related but geographically isolated populations, particularly those inhabiting different islands of tropical archipelagoes.

The taxonomic field has not been slow to exploit the opportunities opened up by the general recognition of the geographical race as a formal taxonomic category, expressible nomenclatorially as the trinomial subspecies. At the present time, it is clear that a great part of the total taxonomic effort is directed toward the detection, characterization, and formal nomenclatorial registration of "new" subspecies. This is particularly true in the case of specialist fields dealing with animal groups in which a large proportion of the full species have already been formally described and named, leaving the burden of the unceasing search for novelties to rest upon the subspecific populations.

The past two decades have witnessed an increasing tendency on the part of taxonomists to rely upon the theoretical basis so firmly promulgated by Mayr. With the progressive accumulation of seemingly sound trinomials in relatively well-worked groups such as the birds, there has grown up a complacency in systematics concerning the objectivity and usefulness of the subspecies. Specialists in many less well-worked groups, and especially those where insufficient time and material are available for detailed analysis of geographical variation, have all but forgotten the early claims of subjectivity for the race, and have come to regard it as a concrete geographical population capable of being recognized by one or a few "diagnostic" characters most accessible for study in preserved material. Many massive revisions have of late depended on the authenticity of this notion.

The tacit but very fundamental theoretical assumption most systematists make is that when characters vary geographically, their variation is co-ordinated. In terms of evolutionary genetics, the predominant genome of a given population constitutes a "coadaptive system," an aggregation of genes which are best adapted as a unit to the special environment of

the population (Ford, 1945). As a result, the geographical distribution of genes, and with them the resultant phenotypes, will be concordant.

While this concept of character concordance follows evolutionary theory well, the factual background from which it is drawn does not rightfully inspire the confidence taxonomists as a group place in it. Taxonomists seem to have forgotten the great complexities and disparities revealed in racial patterns by some really thorough analyses of geographical variation made in the past. Most of the prominent commentators on the theory of speciation have been careful to emphasize the inherently subjective and even arbitrary nature of racial limits. Here is a vastly unappreciated statement by Mayr (1942):

> We have stated repeatedly that every one of the lower systematic categories grades without a break into the next one; the local population into the subspecies, the subspecies into the monotypic species, the monotypic species into the polytypic species, the polytypic species into the superspecies, the superspecies into the species group. This does not mean that we find the entire graded series within every species group. It simply means that in the absence of definite criteria it is, in many cases, equally justifiable to consider certain isolated forms as subspecies or as species, to consider a variable species monotypic or to subdivide it into two or more geographical races, to consider well-characterized forms as subspecies of a polytypic species or to call them representative species.

From our experience in the literature we are convinced that the subspecies concept is the most critical and disorderly area of modern systematic theory—more so than taxonomists have realized or theorists have admitted. Particular confusion surrounds the drawing of the lower limits of the subspecies category within that spectrum of classes recognized by Mayr as extending from "the local population into the subspecies." The difficulties in this delimitation stem from four outstanding features of geographical variation: (1) the tendency for genetically independent characters to show independent geographical variation; (2) the capacity for characters to recur in more than one geographical area, yielding polytopic races; (3) the common occurrence of the microgeographical race; (4) the necessary arbitrariness of any degree of population divergence chosen as the lowest formal racial level. It is our purpose now to illustrate these four features with the aim of re-evaluating the nature of geographical variation and of throwing new light on the subspecies concept as it is applied in taxonomy.

Independent geographical variation. Abundant examples of this phenomenon can be drawn from most careful analyses of geographical variation in a wide variety of animal groups. In his exceptionally complete work on *"Lymantria" dispar*, Goldschmidt (1940) finds eight characters which vary geographically (excluding chromosome size; cf. Makino and Yosida, 1949), none of which is in exact geographical concordance with any of the others. Several of the characters may be used by themselves to make striking racial divisions by cabinet standards, or they may be used in various combinations to achieve different results. Goldschmidt formally establishes five races by utilizing combinations of characters in size and coloration, while at the same time recognizing that "the number of subspecific types could be greatly increased by going into more and more intricate differences." In fact, Goldschmidt's data affirm that the number of races discernible increases as a function of the number of characters taken into consideration. This classic work is doubly important because it illustrates that physiological characters, such as degree of sexuality, rate of larval development, vary geographically just as do the more obvious adult morphological characters ordinarily used in lepidopteran taxonomy.

Moore (1944) surveys variation of the common leopard frog, *Rana pipiens* Schreber, in eastern North America, giving special attention to the characters stressed by authorities who had formerly divided the species into three geographical groups

(species or races). After a very thorough analysis of these taxonomic features plus some others newly introduced, he plots twelve of them in a table of "population formulas" listed geographically. These show clearly that, over broad ranges, there is essentially no consistent maintenance of groupings of characters from one broad region to the next. One can detect gradual clines, step clines, and sudden mid-distribution cline reversals for each character, and the clines obviously do not all have their axes lying along the same compass directions.

One very dramatic character is that concerning the presence or absence of the oviducts in the male. Moore's map (Figure 3) shows oviductless males exclusively inhabiting the Mississippi Basin and the states to the east, from Long Island to northern Florida, while the populations situated peripherally, in the Florida Peninsula, New England, the northern and far western states, and southern Texas have, with scattered exceptions, males with oviducts. It seems reasonable to conclude that the oviductless condition dominates and is spreading outward from some center of origin, gradually displacing the oviduct-present character. The point here is that the distributional pattern of the character shows an obvious lack of correlation with those of the external "taxonomic" features. Is it to be ignored by taxonomists on this account?

Moore later (1946) detailed his findings after conducting interbreeding experiments between frogs from different populations, and found that impairment of embryonic development reached lethal proportions in crosses between parents from the northern and southern extremes of the area sampled, while those populations separated by smaller distances showed intermediate or no hybrid impairment. North-south differences were emphasized in these experiments, but some limited east-west tests gave similar results.

A further extension of his studies led Moore (1949) to consider variation of characters presumably having a much greater adaptive significance than those external ones earlier studied. The new characters included embryonic temperature tolerances and rates of development, which show a north-south difference of a more or less clinal nature; egg size, showing clinal reduction from north to south, but with a striking reversal in Mexico; and form of egg mass, concerning which data were insufficient and show only that variation may possibly run from east to west as well as from north to south. Combining Moore's studies, it is interesting to note that the most promising of the few possible "correlated breaks" in some of the external adult characters comes to the north of New Jersey in the East, whereas by the criteria of egg size and embryonic temperature tolerance, both demonstrated to be adaptively crucial characteristics, the New Jersey populations are not significantly different from the northern populations and belong with the latter instead of with the southern populations.

Moore quite logically rejects the validity of the former broad racial divisions, and points instead to the more uniform concatenation of characters that may be found within each of the many small, allopatric local populations. We agree that his findings accord with his judgement that "there is no generally accepted and easily applied criterion for recognizing subspecies."

LeGare and Hovanitz (1951), in a detailed study of genetically based adult color variation in Californian populations of the butterfly *Melitaea chalcedona* present data suggesting a racial split between the populations of the Little San Bernardino-Mojave Desert mountain area from those to the north and west. However, larval color varies as much as adult color and shows a different geographical deployment. The larvae from several northern populations are yellow, those from the southwest coast are largely deep black, while those from the desert area show replacement of the black by gray. Despite several confused and contradictory statements on the part of LeGare and Hovanitz

with regard to the relationship of color and size, it is clear that these are poorly correlated geographically. Thus all three characters studied tend to vary independently, and as in the case of *Lymantria*, several racial divisions can be drawn depending on which characters are used and in what combinations.

A simple case of discordant variation involving a pair of characters has been described by Mayr (1942) for the bird *Paradisaea apoda*. This species is distributed linearly in the lowlands around the coast of New Guinea. Coloration of the back lightens in a cline extending around the eastern tip of the island and terminating in the north at Goodenough Bay, while coloration of the plumes lightens in a cline which commences to the northwest at Cape Ward Hunt and terminates at the Huon Peninsula. Mayr uses the resultant superimposition patterns to demarcate at intervals five races. One wonders what new racial lines could have been drawn had other, less obvious characters been carefully analyzed.

Polytopic races. If races are delimited by a single character, it is easily within the realm of possibility that this character may be selected to predominance in more than one population of the species. Dice (1940) reports the apparent independent origin of populations of the races *Peromyscus maniculatus rufinus* and *P. m. artemisiae* in western North America; these have arisen through the selection of certain coat color alleles best suited to the color of their environmental background. Cazier (in Mayr, Linsley, Usinger, 1953) has found a similar origin for certain color races in the tiger beetle genus *Cicindela*. We have observed the polytopic occurrence of a distinctive racial character involving appendage length in populations of the ant *Lasius niger* (L.) occupying eastern Asia and the eastern Mediterranean and Atlantic Islands region. Mayr (in the work cited) has expressed the opinion that such populations be recognized under a single subspecific name if no other characters vary geographically to form racial patterns. The extreme taxonomic difficulties arising when the distribution becomes more complex are self-evident and need no further comment here.

The microgeographic race. Even when only one or a few characters are employed by the taxonomist, these often vary so elaborately and extensively that nearly every local population is distinguishable from all the others. The best-known examples of this phenomenon are in the snail genera *Achatinella, Partula, Cepaea, Io, Polymidas, Liguus, Europtis, Orion, Chondrothyra*, etc., the first three of which have been discussed so often in general papers on evolution that they need little additional comment here. The most obvious variation is in shell color patterns, but variation in sculpture, size, coiling, etc., also occurs, and the resultant characters can be used in combination to distinguish endless distinct populations even by the most stringent racial standards.

Microgeographic races are especially prominent in snails because of the sedentary habits of these organisms and their tendency to form isolated local colonies. The same phenomenon is evident in more active animals restricted to habitats of a discontinuous or isolated kind, such as bogs, desert streams, and caves. Examples can be drawn from such diverse groups as butterflies (Higgins, 1950), cave beetles (Valentine, 1945), and *Dendroica* warblers (Hellmayr, 1935; Bond, 1950).

The chief disadvantage inherent in formally recognizing microgeographical races is that regardless of how valid the distinctiveness and internal concordance of their characters may prove them, the list of their trinomials must reach stupendous proportions in time. The result is a top-heavy nomenclature helping little of itself to clarify the nature of the geographical variation, but which instead will certainly obscure it as synonymies are recognized and diagnoses shifted. This is apparently the situation being approached in certain rodent groups. In the pocket gophers *Thomomys bottae* and *T. tal-*

poides a total of thirty-five races has already been recognized from Utah alone (Durrant, 1946), and the area has not been so exhaustively worked as to preclude the possibility that many more races remain undetected.

The microgeographical race as conceived in present evolutionary literature is an unusually well differentiated deme, or local communal population. There is no reason to believe that it is an exceptional phenomenon or anything more than the extreme of the tendency prevalent in all geographically variable species to form local populations of a homogeneous and distinctive genetic constitution. If several independent characters enter into the geographical variation, it is reasonable to assume that many demes can be distinguished by racial standards ordinarily applied in taxonomy if enough of the characters are used in combination. This is in fact the condition described in *Rana pipiens* by Moore, and it is reflected by the many references of geneticists and taxonomists to special "strains" typifying geographical localities.

The arbitrary lower limit of the subspecies. Even when the discrepancies arising from discordant geographical variation are eliminated by the use of one or a very few characters, systematists are faced with the fact that there is no real lower limit to the subspecies category. It has been affirmed repeatedly in a variety of animal groups that racial populations show all degrees of divergence from the lowest level of statistical reliability of mean difference to complete differentiation, with no particular tendency to fall either way. Obviously the only way to resolve this situation taxonomically is to establish an arbitrary lower limit above which populations will be formally recognized as subspecies. This subject has been dealt with thoroughly in the recent text on animal systematics by Mayr, Linsley, and Usinger (1953), and there is no need to treat it in any detail here. The point we wish to emphasize is that no arbitrary lower limit will ever be completely satisfactory, for even if only one character is used, there will always be borderline cases of an extremely vexing nature. Samples defined with vague, untrustworthy characters will often fall above a fixed lower limit, while samples usefully distinguished by striking characters will often fall below it. Furthermore, any hard and fast line will unavoidably produce a condition in which some populations are recognized formally as races while others, essentially of the same constitution but of a slightly lower statistical level, are not recognized.

This difficulty concerning the lower limit of the subspecies is well known to most taxonomists who have devoted much serious attention to the problem. Some have compromised the situation by choosing the level of statistical reliability most nearly conforming to their preconceived notion of what should constitute a valid race in the particular group under study. This appears to have been the procedure followed by Austin (1952), for instance, in his study of Pacific petrels: "A subspecific name designating a geographical population is of no practical use unless at least three-quarters or more of the individuals of that population can be correctly assigned by their morphological characters alone." Austin chooses the "84% from 84%" rule of Simpson and Roe, making the illuminating statement that the "97% from 97%" rule would be too stringent, since "Among the petrels it is rare indeed to find the means of any character separated by two standard deviations, allowing a 97% separation." Austin's method is in no way irregular as modern systematic practice goes, a fact that should signal a general re-examination of the relationship between the "taxonomic intuition" and the choice of hard statistical bases of differentiation.

It is apparent that in their application of the subspecies concept most revisionary workers have misinterpreted the nature of geographical variation as revealed by the more careful analyses in the literature. It is also apparent that taxonomic revisions, using as they do relatively small

samples and usually only one or two independent diagnostic characters, rarely present any valid general information with regard to the nature of geographical variation in its own right. Most formally named subspecies are in effect little more than special cases deduced from the established concept of subspeciation, and their validity is no stronger than the concept itself. For this reason it is important that we do not stop at disclosing the inconsistencies of the concept; rather, we should attempt to revise it to conform as rigorously as possible to fact. From the data supplied in studies such as those by Goldschmidt, Moore, Welch (1938), Crampton (1932), Vanzolini (1951), Brown and Comstock (1952), and others, it is possible to draw several outstanding conclusions having an important bearing on the taxonomic application of the subspecies concept.

1. Where one character varies geographically, other genetically variable characters can be found to vary also.

2. The geographical variation of independent characters tends to be discordant to some degree. The degree of concordance increases with the degree of isolation of populations, but complete concordance from locality to locality is rarely if ever attained. In fact, complete concordance of several known independent characters in an isolated population may (usually?) be a good indication that the population has attained species level. For example, Goldschmidt's *Lymantria dispar hokkaidoensis* shows concordance of at least three characters, more than any other race of this species, but at the same time it appears to be sufficiently cross-sterile with adjacent races to justify recognition as a distinct species.

3. It follows from (2) that the greater the number of characters, the greater will be the total discordance. As a result, the racial lines first drawn from the most prominent "diagnostic" characters will be increasingly obscured or contradicted by the addition of characters, and the situation will be resolved only by either recognizing additional races marked by different combinations of characters, or by recognizing only the major tendencies in concordance. The first of these two solutions, that of recognizing all racial limits by whatever characters can be used to demarcate them by conventional standards, may be the better one in populations that have differentiated *in situ*, i.e., without initial isolation. When this approach is used, the number of distinguishable races has been found in practice to increase at a slightly more than arithmetical progression with the addition of characters used in combination. The second solution, involving the determination of what might be called *peaks of concordance*, seems the more promising where distinguishable populations are totally isolated or are undergoing secondary intergradation. However, since races are then defined according to character peak concordance, nonconforming characters will of necessity have to be omitted, while the extensiveness of the intergrade zones of the species will increase in proportion to the number of characters included in the peaks. The taxonomist will find himself faced with a dilemma: he must either ignore certain poorly conforming characters or else he must incorporate them in his subspecies diagnosis and thereby broaden the zones of intergradation.

4. It would not be too much of a truism to mention that the greater the geographical area encompassed, the less homogeneous will be the population. Conversely, it appears that in geographically very variable species the only thoroughly homogeneous and concordant units, if any exist at all, are the demes (*sensu* Carter, 1951), which tend to be isolated and completely panmictic within themselves. Where clines occur they are marked between but not within these populations.

As noted previously, most taxonomic recognition of subspecies so far has proceeded on the oversimplified "coadaptive system" concept of the race, which assumes that genetically independent characters will tend to be concordant in their geographical variation. We believe that

this assumption has resulted in the establishment of a basic fallacy in the taxonomic method of studying geographical variation. The tendency in this method has been to delimit races on the basis of one or several of the most obvious characters available in preserved material; the remainder of the geographically variable characters are then ignored, or if they are considered at all, they are analyzed only in terms of the subspecific units previously defined. A slight variation of the procedure is to choose several discordant characters, employ them in combinations of two or three to establish racial limits, and then analyze each character individually in terms of these limits.

A case in point is the recent study of the red-eyed towhee *Pipilo erythrophthalmus* by Dickinson (1952). Seven characters are used in various combinations to demarcate four races ranging successively from *alleni* in the south to the typical *erythrophthalmus* in the north. Wing length, plumage and iris color, and tail-spot size vary clinally along the succession of races. Culmen, tarsus, and toe length are greatest in the two intermediate "races" *rileyi* and *canaster*. The total picture of the variation gleaned from this study gives the strong impression that the intermediate forms are nothing more than segments of a broad, partly clinal intergrade zone connecting two extreme terminal populations. This is the conclusion reached by Huntington (1952, *vide infra*) in his analysis of remarkably similar variation found in the eastern purple grackle (*Quiscalus quiscula*); the same kind of characters vary in the same way in both the towhee and grackle, and the intermediate zones in both are geographically very close. The increase in culmen-tarsus-toe lengths in the intermediate towhee populations seems comparable to the increase in culmen-wing lengths in the grackle intergrade zone. In addition, the variation of independent characters in the towhee is obviously quite discordant, as evidenced by the rather poor correspondence of the iris-color distribution as charted by Dickinson with the racial limits previously decided upon.

From Dickinson's data alone it cannot be proved that the geographical pattern in the towhee is the same as in the grackle, and that it may therefore be best expressed by the recognition of two races; yet the fallacy in Dickinson's method of analysis stands out clearly enough. His entire treatment is predicated on the shaky assumption that the races he has defined represent concrete biological units, and this despite his introductory warning: "In ornithological studies in large part the taxonomist is dealing with continuous variates and with variation that appears graphically as a cline. Under such circumstances lines of demarcation must be vague." Having established the four races, Dickinson thereupon uses them as sample groupings from which to analyze each character individually. Only one character, iris color, is plotted geographically as an independent variate. As a result, the true nature of the clinal trends can be inferred only from gross comparisons of the racial diagnoses. Instead of outlining the geographical variation of each character and then synthesizing from it the overall racial pattern, Dickinson has done just the reverse, thereby closing the door to further analysis and interpretation of the data which he has so laboriously gathered and presented.

Because of its closely similar nature and quite different approach, Huntington's analysis of geographical variation in the purple grackle deserves further attention. Much as in the towhee, four races can be demarcated arbitrarily along a southeast-northwest cline, but Huntington chooses to synonymize the intermediate two, *ridgwayi* and *stonei*, as segments of a clinal intergrade zone between the southern nominate race and the northern *versicolor*. Culmen length and wing length vary independently and discordantly with color, this time along a north-south cline. Huntington analyzes these two characters separately to demonstrate that both increase unexpectedly in size (with respect to their

over-all clinal trends) at the zone of intergradation of the color characters. This Huntington suggests may be due to a heterotic effect caused by the secondary intergradation of the two terminal races. By deciding upon the racial units *after* the variation of the genetically independent characters has been analyzed separately, Huntington arrives at what appears to be a more natural classification than that proposed by Dickinson for the towhee. But even more important, his data are presented in such a fashion as to allow ready incorporation into future studies of this species.

Insular Races

The more critical reader may have noted by this time a special condition of the foregoing critique of the subspecies concept: the published analyses of geographical variation that have been considered are in nearly every case concerned with Holarctic continental species. Our review of the literature convinces us that really critical analyses of this sort are virtually lacking for insular populations, and herein rests a point. Much of the background of the modern subspecies concept has been drawn from taxonomic studies of insular and montane groups, all of which are essentially the same in their marked fragmentation into completely isolated populations. Special emphasis in this respect has been laid on birds, and it is not too much to say that the development of the entire theory of geographical speciation has been dominated in large part by ornithological leadership. Yet a survey of ornithological taxonomic literature, including the long series of papers by Mayr, Zimmer, Amadon, Lack, and others (cf. Mayr, 1951), has convinced us that the morphological and distributional data on relevant bird populations leave much to be desired, and in fact offer very little definitive information on the two central topics, independent character variation and the subspecies-species evolutionary transition, as they apply to insular populations.

This literature is characterized by two outstanding shortcomings. First, a very limited number of characters is used; taxonomic revisions are typically based on studies of variation in size, external proportions, and color. Even the detailed analyses of (continental) geographical variation, such as those by Dickinson and Huntington just discussed, are based on these same few characters. To these we may add Miller's well-known *Junco* revision, which is the most thorough of all such studies on birds known to us. We have already stressed the weaknesses of any infraspecific classification based on limited numbers of characters. It would be of the utmost interest to see an ornithological revision employing the same number and kinds of characters studied by Goldschmidt in *Lymantria* and Moore in *Rana;* these might include internal features, egg color and size, morphological and physiological nestling characters, microscopic barbule structure, epidermal sculpture, and many others. This sort of work may well be rendered unduly difficult by the limitations of standard ornithological materials and methods, and it would perhaps be presumptuous to suggest a shift of technique. Nevertheless, it is important to emphasize the little-appreciated point that ornithological studies do not remotely approach in morphological detail those published on some other groups of animals.

The second shortcoming of ornithological revisions is the paucity of data on the subspecific versus specific status of insular and other isolated populations. It is true that sharp character discontinuities are often set from isolate to isolate; this allopatric pattern occurs in so many groups as to create a striking faunal picture, especially in tropical archipelagoes. Again we need to point out that few characters have been determined to participate in the discontinuities, and little information has been obtained on concordance of variation, especially as it occurs between islands and island groups. Furthermore, it is a fact that many of these striking racial differ-

ences are based on limited samples (occasionally consisting of a single specimen) which may have originated from the same immediate locality or even from a single clutch. There is no way of knowing, on the basis of the mass of published taxonomic work, whether or not the study of additional, less obvious, and possibly discordant characters in larger bird samples might reveal alternative racial divisions among island groups, and finer divisions on single islands, such as occur in snails and probably in other animal groups.

A stronger aspect of this shortcoming is seen in the other direction. Where the several characters utilized show marked concordance, there is always the distinct possibility, previously mentioned, that the allopatric populations have already attained species level. A certain amount of evidence is accumulating to indicate that this may be a very common phenomenon. We have already mentioned the example of Goldschmidt's *Lymantria dispar hokkaidoensis*, which, showing a high degree of character concordance, is partially cross-sterile with adjacent populations. Kinsey (1936) describes four pairs of sympatric species of the *Cynips dugèsi* complex in southern Mexico, none of them more strongly differentiated than are the numerous isolated populations to the north; the extreme paucity of hybrids between the northern allopatric populations may be taken as additional support for the contention that they really represent member species of a superspecies, notwithstanding the high degree of isolation. Most edifying, however, are the numerous cases cited in the literature of pairs of closely related species with contiguous or narrowly overlapping ranges. Taxonomists often consider such pairs to be races of a single species until their true relationship is verified by a careful investigation of their interaction in the zone of contact. The significance of this particular kind of taxonomic clarification has been reviewed for ornithology by Mayr (1951), who uses the expression "pseudo-conspecific pairs of allopatric species" to refer to pertinent cases.

Summing up, we must affirm that present knowledge of insular races, including those of birds, is actually too limited to allow close comparison with the patterns elucidated in studies of continental races. While it is true that striking discontinuities often occur between island or other isolated populations, any interpretation of these discontinuities must carry two serious qualifications. First, insular races, like most continental races, have been defined on the basis of limited numbers of characters, often in assorted combinations, without consideration of the possibly discordant variation of other, more cryptic characters. Second, where some degree of concordance is demonstrated, the excellent possibility that the populations have already attained species level has very seldom been ruled out.

Subspecies: the Taxonomic Application

Because the geographical race has a demonstrably flimsy conceptual basis, it is unfortunate that it has become through the years a deeply rooted taxonomic resort. That the race has become so integral a part of our systematics is due largely to the circumstance that, under the more hierarchical-sounding alias "subspecies," it has established itself gradually but ever more firmly as a unit that could and should be dignified with a Latin name. Caught up in the wave of enthusiasm for the new systematics, the International Commission of Zoological Nomenclature, meeting at Paris in 1948, gave its most recent formal sanction to the named subspecies at the same time that it quite rightly consigned the "variety" and other minor categories without geographical connotation to an inferior rank. In effect, the Commission again officially recognized subspecific names on a level of availability with those given to full species insofar as priority is concerned, and again gave formal recognition to the employment of the neo-Linnaean trinomial. The pool of

available trivial names, many of which may never prove assignable to definite species, has been more firmly fixed at discouragingly vast proportions by this action.

If it is now clear that the subspecies trinomial is fast becoming an unquestioned and traditional fixture, it is equally clear, at least to us, that in its assumed function as a formal means of registering geographical variation within the species it tends to be both illusory and superfluous.

Mayr sums up our general philosophy perfectly in his very recent (1953) advice, offered in a different connection to those in attendance at the birth of a struggling taxonomy of viruses:

> The history of all classification, whether dealing with inanimate objects or with organisms, shows that early attempts of classification are based on superficial similarities and very often on single characters, while all improvements of classification are due to ever more penetrating analysis and a broadening of the basis of classification by including more and more characters. The soundest classifications are those built on the greatest possible number of clues. Reciprocally, it can be stated that, in sound classifications, there is usually a fair concordance of the various characters.

The application of this logic to our present knowledge of geographical variation cannot fail to stir a feeling that the trinomial has outlived its usefulness in taxonomy. We are encouraged to note that ornithologists have been among the first to apprehend this circumstance. Lack (1946), after grappling with trinomials in the European robin and finding them based uneasily on convergent polyphyletic characters and complex clinal trends, concludes:

> The use of subspecific names not only implies discontinuity where none may exist, but also unity where there may, in fact, be discontinuity. . . . Certainly, in the case of *Erithacus rubecula*, it is both simpler and more accurate to describe subspecific variation in terms of geographical trends, and to omit altogether the tyranny of subspecific names.

Mayr (1951), in reviewing twelve years of progress in the study of bird speciation, observes, "Instead of expending their energy on the describing and naming of trifling subspecies, bird taxonomists might well devote more attention to the evaluation of trends in variation."

We are inclined to feel even more strongly about the situation. We are convinced that unless our own sampling of the taxonomic literature has badly deceived us, we shall soon begin to observe the withering of the trinomial and its cumbersome appurtenances—the types, the tinted labels, the ponderous subspecies lists gravely entered in a thousand catalogues, the awkward labelling of masses of "intergrade" specimens, and all of the other procedural details that so unnecessarily consume the few effective working hours a modern taxonomist has. We anticipate the time when the taxonomist, if he wants to apply a formal Latinized name to his sample, will have first to produce indications that the population represented has the characteristics of a species. The more irresponsible or naive worker will not then be able, after a weak gesture in the direction of systematic study, to retire to the comfortable, safe nebulosity of a subspecies designation under a name having guaranteed availability against the future contingency that someone will perform the labor necessary to define a good species fitting his type. The study of geographic variation may eventually become just what the term implies, and not merely remain the subspecies mill it so largely is today.

The possibility that some International Congress not too far in the future will see fit to relegate unborn subspecific names to the nomenclatural limbo now occupied by the variety, the natio, the aberration, the forma, etc., inevitably brings up the question of the kind of reference shorthand we shall need to aid in the description of geographical variation. Fortunately, all the reference we require for this purpose is contained in (1) the correct determination to species, and (2) the locality and ecological data that will have to accompany any specimen worth studying. Thus, in publications, we can speak

of "*Rana pipiens* Schreber, Montauk Pt., New York"; or "*R. pipiens*, southeastern corner of J. B. Smith farm, 5 miles west of Montauk Pt., in cattail swamp"; or even "*R. pipiens* from Long Island," ". . . from the East Coast," and so on. The precision or breadth of the geographical designation will vary according to the needs of the investigator and with the actual geographical distribution of the character or combination of characters under study. Inevitably, perhaps, repeatedly discussed populations will come to be referred to as "Montauk A," "Reelfoot Lake," "Rock Island," and so forth, but this will no more prove a pitfall than is the geographical vernacular familiarly applied to "strains" of *Drosophila virilis* (Patterson and Stone, 1952), or the locality names by which experienced trappers can often distinguish a series of pelts.

If a character combination of a population remains at all co-ordinate and consistent in its territorial occupancy, there is every reason why we should refer to it merely by mentioning the species concerned and either the locality or full distribution that it occupies. There is no evident advantage in the use of the recommended form "*montaukensis*" over "Long Island race" or "Montauk A." If we find at Lhasa a population of mice of known species that carries a distinctive black cheek stripe, the name "*lhasensis*" conveys this no more readily than does "Lhasa race." If it subsequently be found that the entire Tibetan Plateau is inhabited by mice carrying black cheek stripes, "Lhasa race" is readily expanded, so that we can speak of the "Tibetan race" just as easily as, and interchangeably with, "Lhasa race." The city of Lhasa remains a feature of the Tibetan Plateau, and so do the black-cheeked mice of both places. The very informality and flexibility of a vernacular system are among its most appealing characteristics. A geographical vernacular designation lacks the esoteric authoritarianism surrounding the Latin trinomial, but it is this very quality of trinomials that we consider most misleading, cumbersome, and generally repellent, especially to the uninitiated. The geographical vernacular is more broadly communicable, more frankly expressive, fully as mnemonic, at least as certain in the long run to be precise, and it cuts the taxonomic red tape to practically nothing. Its present unostentatious use in many individual papers in several taxonomic fields reveals no serious operational drawbacks. In short, we feel that the facts we have outlined call for serious, conscious consideration of the desirability of eventual abandonment of the subspecies trinomial and its replacement by a system of reference based on the vernacular employment of relevant geographical names.

Summary

1. Mayr's criterion for the species, that of free interbreeding of populations in nature, when qualified by the conditions of sympatry and synchrony, and extended by morphological analogy to isolated populations, has proved to be objective and practicable for taxonomic work.

2. Roughly, the subspecies has been defined as a genetically distinct geographical fraction of the species. The assumption has been followed, tacitly or otherwise, that when secondary characters vary geographically, this variation tends to follow whatever "diagnostic" characters are chosen to delimit races, and that the subspecies in general can be shown upon further analysis to be a concrete unit. This assumption is demonstrated herein to be contravened by the data available in the literature dealing with geographical variation.

3. Three other prominent features affecting the subspecies concept render it even more subjective and arbitrary in taxonomic practice: the polytopic race, the microgeographic race, and the artificiality of quantitative methods of defining the formal lower limits of the subspecies.

4. Most taxonomic analysis at the intraspecific level has been directed toward the end of naming and characterizing new

subspecies. This tends to be an inefficient and misleading method. It is felt that geographical variation should be analyzed first in terms of genetically independent characters, which would then be employed synthetically to search for possible racial groupings.

5. Although "insular" races (as opposed to contiguous "continental" races) appear at times to be exceptionally clear-cut and have been extensively used in generalizations on raciation, the data in most available analyses are in all respects insufficient to evaluate the intricacies of this process. It is not even certainly known in most such cases whether distinctive isolated populations are races or species.

6. We feel that as the analyses of geographical variation become more complete, the trinomial nomenclatorial system will be revealed as inefficient and superfluous for reference purposes. It is suggested that, for the study of such variation, the use of the simple vernacular locality citation or a brief statement of the range involved is adequate and to be preferred to the formal Latinized trinomial.

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Cushman Foundation for Foraminiferal Research

The Cushman Foundation for Foraminiferal Research, Inc., was organized in June 1950 in the District of Columbia for the purpose of continuing work initiated by the late Dr. Joseph Augustine Cushman, who founded the Cushman Laboratory for Foraminiferal Research at Sharon, Massachusetts, in 1923. The Foundation is a private organization, the purposes of which are the promotion of research in the paleontology and biology of the Foraminifera and related organisms and the publication of the results of such researches.

From 1925 to the death of its founder and Director, the Laboratory was operated as a non-profit organization for scientific research in cooperation with the U. S. Geological Survey and the U. S. National Museum and for advanced study in cooperation with Harvard University, Radcliffe College, and Massachusetts Institute of Technology.

For twenty-five years, from 1925 through 1949, the Laboratory published a quarterly journal, the *Contributions from the Cushman Laboratory for Foraminiferal Research*, devoted to papers on Foraminifera written by Dr. Cushman and his many students and collaborators.

Following his death in 1949, the journal was concluded with its 25th volume. Slightly over a year later in August 1950, the then newly organized Cushman Foundation issued the first number of Volume 1 of the *Contributions from the Cushman Foundation for Foraminiferal Research*, a quarterly established to continue the earlier *Laboratory Contributions*. This new periodical is patterned after the old one, but its size and scope have been enlarged. Its publication facilities are open to all serious students of the Foraminifera and allied organisms.

Two annual volumes have appeared under the editorship of Alfred R. Loeblich, Jr. Volume 3 (1952) has been prepared under the editorship of Hans E. Thalmann, P. O. Box 1978, Stanford University, California. The Editor welcomes manuscripts for publication embodying the results of foraminiferal research in all its phases: biology, paleontology, ecology, taxonomy, and use in stratigraphy.

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Life-History Studies in Insect Systematics

CHARLES D. MICHENER

IN PREPARING this paper I have taken "life history" to mean not only the bionomics of insects, but also structural features of immature stages. Except for characters which can be detected only by physiological investigation, this means the whole gamut of characteristics not readily studied by the average systematist because they are not structural features of the stages usually preserved in collections.

Behavior

It is the general tendency among systematists to pay less attention to characteristics of behavior than to structural features. This is partly due to the fact that behavior requires long periods of study; an observer must make his observations at the right season and at the right place, and often all sorts of difficulties prevent or delay the observations. No one student can make critical observations on very many species. Because of the possibility of preserving specimens, these difficulties do not stand in the way of morphological observations. A second reason for paying less attention to behavior patterns is that many students have regarded them as more variable than structural characters. Nonetheless every zoologist recognizes that certain features of behavior often characterize whole groups of animals. The literature is full of statements of behavior pertaining to whole families or genera. Such statements reflect our confidence in these characteristics as group features, that is, features of certain phyletic lines. In this paper emphasis will be centered on evidence which behavior studies contribute to phylogeny, although differences in behavior between closely allied forms are also interesting, especially if these differences include possible isolating mechanisms. It is often remarkable what seemingly minute characteristics of behavior are common to members of large groups, even though some conspicuous features may vary widely. The following example illustrates the remarkably minute details in behavior occurring presumably throughout a family of non-social bees.

Recent observations on nest provisioning and egg laying of three unrelated genera of Megachilidae show a pattern that is consistently followed. On returning to the cell from a foraging trip, the female enters head first, deposits nectar in the cell, then backs out (in one genus all the way out of the nest, in the others merely out of the cell), turns around, backs in, and deposits her pollen load in the cell. She then departs on another foraging trip. On returning from the last such trip for a particular cell, she enters head first, deposits the nectar, backs out, turns around, backs in, deposits pollen, crawls out, turns around, goes in head first and perhaps puts the pollen mass in its final form, backs out, turns around, backs in, lays an egg, crawls out, turns around, re-enters the cell head first for a moment, then backs out and departs on a trip on which she will obtain material to close the cell. These minutiae of behavior were alike in all forms studied and different from comparable behavior in other families of bees. They are alike even though many other aspects of the behavior of these three genera are very different. This is reminiscent of numerous examples in which minute or inconspicuous morphological features indicate certain relationships, presumably correctly, while various striking and conspicuous features fail to do so, and are therefore commonly called superficial.

No zoologist can doubt that characteris-

tics of behavior evolve just as do characteristics of morphology. Laboratory evidence of this exists; for example, Dr. Robert R. Sokal of the University of Kansas has developed a strain of *Drosophila melanogaster* Meigen in which pupation at the periphery of the larval medium is much commoner than in the parental stocks. This change in behavior accompanied development of DDT resistance in the larvae of these flies, but is evident even when the flies are grown in the absence of DDT.

In the field, there is evidence of similar developments in rather short time periods. For example, "resistance" of codling moth [*Carpocapsa pomonella* (Linnaeus)] larvae to lead arsenate evolved in a few decades, and results, not from actual physiological resistance, but from a change in larval behavior. The resistant strain burrows directly into the apple while the nonresistant strains nibble here and there and thus have a greater chance of becoming poisoned before burrowing (for a review of this and other matters concerning the resistance of insects to insecticides, see Babers, 1949, and Babers and Pratt, 1951).

Further evidence that behavior evolves in a manner similar to morphological characters can be obtained from apparent phylogenetic series of behavior characteristics. Spieth (1952) has shown presumed phylogenetic series based upon mating behavior among various species of *Drosophila*. In a general way these series parallel those based on morphological characteristics. Emerson (1938) gives numerous examples of the phylogenetic significance of nest structures in termites. An excellent example of apparent phyletic series is provided by the nests constructed by African termites of the genus *Apicotermes* (see Emerson, 1950). The nest structures can be arranged in a branching series which resembles a phyletic series based upon structures of organisms. It seems likely that homologous behavior patterns produce the apparently homologous nest structures and that evolution of the patterns resulted in the evolution in nest structures and therefore in the phyletic series represented by Emerson. Schneirla (in Emerson, 1950) challenges this idea, however, on the basis that the behavior patterns have not been studied and different behavior patterns might produce similar structures. This seems unlikely in view of the complexity of the nest structures concerned.

The establishment of relationships and of phylogenetic systems with the aid of behavior characteristics implies studies of comparative behavior just as the use of morphological characters for this purpose implies studies of comparative morphology. Lorenz (e.g. 1950) has written extensively on comparative behavior, that is, the similarities and dissimilarities of homologous aspects of behavior, as have others of the Lorenz-Tinbergen group (see Tinbergen, 1951). Schneirla (1952) has criticized this approach, pointing out an apparent error by Tinbergen and his associates in the interpretation of the gaping reaction of young thrushes and cautions that similar behavior patterns in widely different animals are not necessarily homologous and that comparative studies ought to be concerned with the ontogeny of the characteristics studied, in order that homologies can be definitely established. (Schneirla seems to avoid carefully the use of the word homology in connection with behavior.) Any comparative morphologist will agree that similarities in widely different animals do not necessarily indicate homology and that homology can usually best be established with the aid of ontogenetic or phylogenetic studies. We must essentially agree with Schneirla's cautious approach.

It seems obvious, nevertheless, that the idea of homology is useful and necessary in connection with behavior. If it is not, the thought of recognizing phyletic series in behavior patterns is untenable and the idea that systematists can make use of behavior in understanding relationships among animals vanishes. Partly because of individually learned aspects of behavior, homology may be more difficult to

establish in the case of behavior than in the case of structure, but this is no reason to give up the attempt.

From the standpoint of genetics and evolutionary theory, there should be no objection to accepting behavioral homologies. Genes influence physiological processes; some of the latter affect structures or materials such as pigments, others affect innate behavior or the potentialities for learned behavior. No doubt many genes affect both behavior and structural features. An example is the "pallid" gene of the housemouse, which influences posture and gait as well as coat color and the otoliths of the utriculus (Grüneberg, 1952). Other examples appear in the work of Williams and Reed (1944) who studied wing-beat frequencies of various mutant strains of *Drosophila melanogaster*. They found that in 45 per cent of these strains the frequencies differed significantly from those of a control (wild type) strain and that with other mutants flight did not occur at all even though the wings were apparently normal in structure. These authors consider the genetic evidence and conclude that in at least some strains the effect on flight is assignable to the mutant genes rather than to accompanying genes. Had such pleiotropic genes become established as characteristics of genera or higher categories, it would plainly be absurd to speak of their morphological manifestations as homologies and fail to do likewise for their behavioral manifestations.

In summary, then, since features of behavior obviously evolve and since behavioral homologies can sometimes be recognized, the field of comparative behavior ought to be investigated much more thoroughly than in the past as it could yield much of interest to systematists.

Host Specificity

A group of behavioral or ecological characteristics which require special attention are those related to host specificity. These characteristics are presumably not fundamentally different in their basic significance to systematists or in their evolution, from a multitude of other characteristics. They deserve mention here only because more is known about them than about most bionomic characteristics, for collectors often record the hosts upon which they obtain specimens. The following comments are based upon the bees, the group with which I am most familiar, but it is believed that the principles involved would apply equally to any group. Among bees, specificity is demonstrated principally in pollen collecting. Most species will suck nectar from many kinds of flowers. Forms which gather pollen from many kinds of flowers are termed polylectic; forms which gather pollen from a few, usually related kinds of flowers are called oligolectic.

Some bees show obvious morphological adaptations to particular kinds of flowers. For example, in all species of the genus *Proteriades* (Megachilidae) and in certain species of *Andrena* (Andrenidae) there are hooked hairs on the proboscis which enable these bees to drag pollen out of the flowers of *Cryptantha*. These flowers are so small and the stamens so short that pollen cannot be gathered with the legs in the ordinary way (see Timberlake and Michener, 1950). These bees are oligolectic on *Cryptantha*, never having been observed to take pollen from any other plant. Another example is found in *Diadasia*, most species of which have pollen-collecting hairs adapted to holding particularly coarse pollen. One group of related species gathers exclusively the pollen of such malvaceous genera as *Sphaeralcea* and *Sida*, while another group of related species gathers the equally coarse pollen of cacti. The importance of this knowledge to the systematist is obvious.

In the great majority of oligolectic bees, however, there is no obvious morphological adaptation of the bee to the flower. In some cases allied species collect pollen from the same flower species, or from several species of the same genus of flowers, as in the genera *Proteriades* and *Diadasia* mentioned above. This behavior

suggests that geographical speciation occurred on the same host. In other cases allied species occur on different and often unrelated hosts, probably indicating geographical speciation in which differences in host preference have become associated with other specific characters.

It should be of interest to systematists to consider some reasons for host specificity. It might seem that nonspecific or polylectic species would be at an advantage compared with narrowly specialized or oligolectic species because they would be able to make use of more sources of food, their distribution would not be limited by that of their hosts, and environmental changes which might eliminate the host of an oligolectic form and thus exterminate it might leave a polylectic species unaffected. In spite of these apparent advantages of the unspecialized food habit, oligolectic species or groups of bees have arisen repeatedly from polylectic ancestors; indeed specialization is a general biological rule, only rarely reversed. From this it is obvious that progress toward oligolecty must be advantageous as long as the proper environment is present. Such progress serves to remove species from competition with one another, as is suggested in the following paragraph.

Among any group of polylectic species competing with one another for pollen supplies, one species will in all probability be at least slightly better adapted for obtaining its pollen from one flower while others will be better adapted to other flowers. For example, let us suppose that species I is better adapted to obtaining pollen from flower *A* than from other flowers, while species II is better adapted to flower *B*. In this instance individuals of species I visiting flower *B* will be at a disadvantage as compared with those visiting flower *A*, because of the potent competition provided by species II on the flower to which it is best adapted. Therefore, selection will be against those individuals of species I visiting flower *B*. If, because of inherited characteristics or preimaginal conditioning, bees which visit flower *A* tend to produce offspring which visit flower *A*, there will be a tendency for the first species to restrict itself to flower *A*. Thus competition between the species is reduced. If by a like process species II restricts itself to flower *B*, the two species will no longer be in competition with one another.

These ideas were elaborated by Robertson (1899, 1914) at a time when current ideas on evolution were unknown. More recently those who have followed Gause's ideas (1934) have concluded that species with the same ecologies cannot persist together in the same region and that species with broadly overlapping ecologies will tend to evolve so as to reduce competition with one another (see also Lack, 1947, 1949). These ideas have been in part tested experimentally by Park (1948) and recently by Moore (1952).

It is interesting to examine this theory of the origin and significance of oligolecty in the light of the climatic and floral characteristics of various parts of the world. If this theory is correct, one would expect the greatest percentage of oligolectic bees in regions, such as deserts, where most of the numerous kinds of flowers bloom during a brief season. Many species of bees would be in competition for the pollen supply were it not for oligolecty. The competition would be particularly intense during the frequent dry years or series of years when only a few plants of any one species bloom and the pollen supplies are therefore limited. In contrast, one would expect a minimum of oligolecty in regions, such as the tropics, in which, because of the relatively uniform climate, flowers appear in succession throughout the year and most of the species of bees have a long season of flight, frequently so long that no one flower blooms for a long enough season to permit oligolecty.

Accurate statistics on the frequency of oligolecty in various regions are not available because of the inadequacy of the studies in most regions and because of

the poor definition of the word oligolecty itself. (How restricted in its pollen collecting must a bee become to be called oligolectic?) It is evident in spite of these difficulties that the percentage of bee species which are oligolectic in the tropical fauna is far less than that in arid regions such as the southwestern United States.

Another possible explanation for the low percentage of oligolecty in the tropics may be simply that those groups of bees (e.g. the Andrenidae, especially the subfamily Panurginae) which account for much of the oligolecty of the deserts are not well represented in the tropics. However, groups which have numerous oligolectic species occur in most of the families and subfamilies of bees in the southwestern deserts; this is not the case in the tropics. Perhaps such groups consist of species particularly sensitive to competition for pollen.

Characters of Immature Stages

One of the outstanding features of the holometabolous orders of insects is that the immature stages are utterly different from the adults, not only in superficial appearance but in fundamentals of structure and way of life. In general the characters which distinguish the larvae of closely related forms are less obvious than those which distinguish the adults, but this is not always the case; sometimes larval characters are more conspicuous than those of the adults. Partly because of the adaptation of larvae to special habits, larval characters distinguishing certain higher groups (e.g. families) are much more conspicuous than those distinguishing adults. Larvae often provide characteristics which are useful in interpreting the relationship of insect groups.

Certain general problems concerning larval forms which have been more or less evident for many years are perhaps worth brief consideration here. The main problem is, how does it happen that larvae can evolve in quite different directions and at different rates [1] from adults, adapting themselves to different food requirements, habitats, and the like?

As is now well known, mutations affect processes, and only indirectly characters. A given process may occur at any stage of development. A mutation that affects a process influencing only a certain portion of the development might affect larval characters principally, since the cells which will become adult structures are segregated into primordia which do not develop much until larval life is well along, or it might affect only adult characters if its influence is not felt until late in development. A mutation may affect a process influencing characters of selective value in one stage (e.g. the larva) and other characters of little selective value in another stage. It may influence characters visible phenotypically and externally in one stage, but not in the other.

From this it is evident that there is a basis for the appearance and subsequent selection of characters of one stage in the life history, with little visible effect upon other stages. Of course, since larva and adult are the same individual, selection will depend upon success in both stages; it cannot act independently on either. Fundamentally the situation is little different from that which makes it possible for the young of animals without metamorphosis to have distinctive features (e.g. immature plumages of birds, spots on young deer) different from those of the adult and subject to their own partially independent evolutionary development.

The segregation of larval from adult characters is exaggerated, however, in holometabolous insects. Perhaps this is possible in part because, at least in *Drosophila* and *Tineola,* larval and adult structures are determined at different times during development. Thus there is a time

[1] As to rates, it must of course be remembered that what is meant is rates of phenotypic evolution; there can be no differences in rates of true or genotypic evolution between larvae and adults.

when minor injuries to the egg surface will cause larval but not adult defects, a later time when they will cause adult but not larval defects. (For a brief summary of our knowledge in this connection, see Wigglesworth, 1950.)

Rapid evolution of one stage, without comparable phenotypic change in the other, or with phenotypic changes having no obvious selective value in the other, is not fundamentally different from another common phenomenon, namely rapid evolution of one structure or group of structures while the others remain little changed. In this light it is easy to see that larval characters, and bionomic characters as well, are merely more characters, of no more systematic value and of no less than conventionally used characters. It is obvious, however, that larval characters are often of great interest as indicators of the environmental forces that have been in operation, for the larvae often occupy specialized habitats and exhibit various striking morphological adaptations to them.

Discussion

It is clear that any genetically controlled characteristic is subject to the interplay of the principal evolutionary forces, mutation pressure and selection pressure. Hence it will have evolved. This is true whether its phenotypic expression involves structure, behavior, or some physiological process having no influence on structure or behavior, and it is true no matter how minute the characteristic may appear to be. One of the principal aims of systematics is to obtain information on evolution or phylogeny, and the hierarchy of taxonomic categories is designed to summarize such information in a convenient form. Since all characters evolve, as many as possible (it is plainly impracticable to study all) should be considered in investigating the phylogeny of any group. Largely because of parallelisms, classifications based upon very few characters are often artificial. It follows, then, that the more characters considered in devising a classification, the greater the likelihood that the classification will represent the true phylogeny. It is, therefore, important that systematists search for characters of all sorts, whether they are morphological or bionomic.

In the last decade or two systematics has taken on important new meaning, particularly at the species level and below, as the knowledge of genetics and that of systematics have become co-ordinated. The great need now is for tools to make possible similar advances at the level of the higher categories. As more and more characters are found and studied in accordance with the conclusion of the preceding paragraph, the correlations among the multitude of characters often become so complex as to make analyses difficult or impossible. Thus certain characters may suggest one relationship while others suggest quite different ones. When methods are devised for studying these sets of correlations satisfactorily, we may hope for important advances in our understanding of systematics and evolution.

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The Natural Classification of the Rhombognathinae (Acari, Halacaridae)

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THE Rhombognathinae are a group of herbivorous Acari inhabiting intertidal and shallow subtidal marine and estuarine waters. The group is cosmopolitan in distribution, although some of the genera are not, *Rhombognathides* Viets 1927 and *Metarhombognathus* Newell 1947 being known at present from only the temperate North Atlantic Ocean and adjacent subarctic or arctic waters.[1] The genus *Rhombognathus* Trouessart 1888 is certainly cosmopolitan, and the genus *Isobactrus* Newell 1947 is probably so, being known from the North Atlantic, Adriatic Sea, the Kerguelen Archipelago, and the North Pacific Ocean. The latter record for the genus *Isobactrus* is based on undescribed species from the western United States and the Aleutian Islands.

The subfamily was erected by Viets (1927, pp. 87–89) to include the single genus *Rhombognathus,* which was divided into three subgenera: *Rhombognathus s. str.* Trouessart 1888, *Rhombognathides* Viets 1927, and *Rhombognathopsis* Viets 1927. The subdivision was based solely on the number of claws on the tarsi. In the course of studies on the Halacaridae of eastern North America, the present author (1947, pp. 25–33) developed a new system of classification which produced a more natural grouping than Viets' system, and the four natural groups were considered to constitute four distinct genera. At that time the writer presented morphological evidence which was deemed adequate to justify the revision, and while the evidence presented was not exhaustive, the revision appeared to justify itself by the results produced. Apparently it did not, however, for this system has been reviewed critically by Viets (1950, pp. 18–19; 1952, pp. 97–101), who rejected the conclusions of the author and placed the genera *Isobactrus* and *Metarhombognathus* in synonymy with *Rhombognathus* and *Rhombognathopsis,* respectively.

The vigor and thoroughness of Viets' defense of his classification, whether well founded or not, would lead the casual reader to assume that the present writer's system was not only unproved, but quite certainly erroneous. This is especially so in view of the fact that Viets has seen and named more species of Halacaridae than anyone else, and conceivably could be more familiar with the morphology of the group than any other worker. Thus we are provided with an opportunity to compare two systems of classification, each of which is claimed by its author to be the more natural. The case is made interesting beyond the limits of this particular group, since these mites possess a wealth of structural variation of supraspecific order, making it possible to apply quasi-statistical methods of comparison. The writer feels that these will be of interest to others faced with similar problems. There is little that is basically new in the methodology; it is primarily a formalization of the procedural logic used by all systematists, with varying degrees of success, in attempting to achieve a natural classification. In the following account,

[1] *Rhombognathides trionyx* (Trouessart) 1900 has been reported from the French Atlantic Coast and Tierra del Fuego. Such a distribution, in a genus restricted to depths less than 50 meters and with no known representatives in the intervening tropics is so unusual as to require verification. Possibly a contaminant or a mislabeled slide is involved here.

the writer will first discuss those morphological characters which are of greatest stability in the Rhombognathinae, and then will analyze the distribution of the variants of those entities in the known species.

Characters and Character Variants in the Rhombognathinae

A *character* is defined as any structural, physiological, ontogenic, or other feature; e.g., dorsal setae, preocular setae, degree of armoring, adanal setae. A *variant* or *character variant* is the particular expression of the character found in a given form; e.g., dorsal setae numbering nine pairs (as contrasted with five pairs), preocular setae in ocular plate (or in the membranous area between the ocular plate and anterior dorsal plate), armor undergoing a reduction in final molt (as contrasted with a continued increase), adanal setae present (as contrasted with absent).

In the discussion of characters, the writer will use those binomials employed by him in the monograph on the Halacaridae of eastern North America. While this ostensibly presupposes the outcome of the analysis, to do otherwise would result in needless nomenclatorial confusion. The only alternative is to use species names alone, without generic designations, a procedure which likewise results in confusion whenever it is followed.

In order to discuss the body chaetotaxy of these mites, it is necessary to adopt a system of nomenclature and a convenient symbolism. The body setae will be divided into six series: dorsal, anterior epimeral, posterior epimeral, perigenital, subgenital, and adanal. The dorsal setae (*ds*) are those in the anterior dorsal plate (*AD*), the ocular plates (*OC*), posterior dorsal plate (*PD*), and the associated membranous area. The anterior epimeral setae (*aes*) are those of the anterior epimeral plate (*AE*), while the posterior epimeral setae (*pes*) are those of the posterior epimeral plates (*PE*). The perigenital setae (*pgs*) are those of the genital plate, while the subgenital setae (*sgs*) are those included within the genital opening itself, or on the sclerites covering the opening. The adanal setae (*adans*) always consist of a single pair in known Halacaridae, or are rarely absent.

The following is a list of the symbols employed in the discussion and the accompanying figures:

adans: adanal setae.
aes-I: the seta(e) of coxa(e) I of the anterior epimeral plate.
aes-II-lat., and *aes-II-v*: the lateral and ventral seta(e), respectively, of coxa(e) II.
aes-II-adj: adjunctive setae of anterior epimeral plate (borne on coxa II).
ds-adp: dorsal series, setae of anterodorsal plate.
ds-proc: dorsal series, preocular setae.
ds-loc: dorsal series, laterocular setae.
ds-poc: dorsal series, postocular setae.
ds-ioc: dorsal series, interocular setae.
pes-III-lat, and *pes-III-v*: lateral and ventral seta(e), respectively, of coxa(e) III.
pes-III-adj: adjunctive seta(e) of coxa(e) III.
pes-IV: the seta(e) of coxa(e) IV.
pgs: perigenital setae, on *GA*.
sgs: subgenital setae, on genital sclerites.
AD: anterodorsal plate.
AE: anterior epimeral plate.
GA: genitoanal plate.
OC: ocular plates.
PD: posterodorsal plate.
PE: posterior epimeral plate(s).

Dorsal setae (*ds*). The Rhombognathinae fall into two sharply separated groups with respect to the dorsal chaetotaxy. In adults and nymphs of *Rhombognathides pascens* and *Metarhombognathus armatus americanus*, there are nine pairs of setae in the four dorsal plates and surrounding membranous areas. These may vary in position according to species and stage of development, but the basic pattern is the same and the setae can be homologized without question (Fig. 1, *3, 4*). The anterodorsal plate bears a single pair of setae (*ds-adp*) as in all Halacaridae. Then follows a group of setae which will be identified by their position relative to the corneae. In both species there is a pair of setae between *AD* and the corneae. This pair is found in all species of Hala-

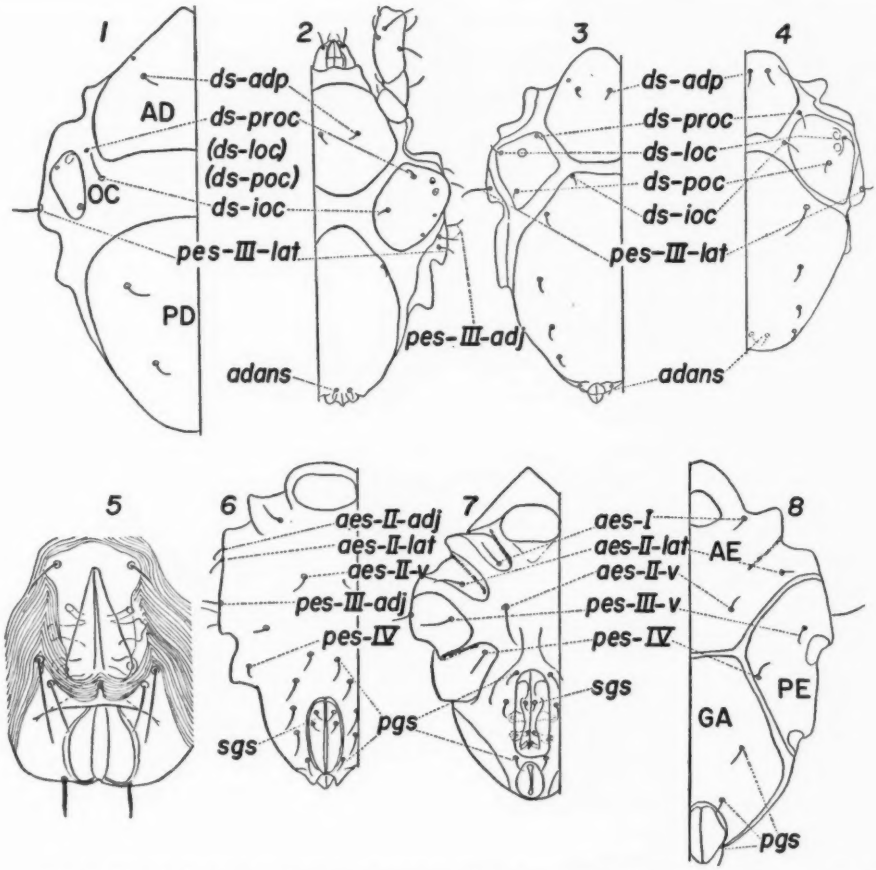

FIG. 1. Morphological characters of systematic value in the Rhombognathinae. *1, Isobactrus setosus,* female, dorsum; *2, Rhombognathus magnirostris,* female, dorsum; *3, Rhombognathides pascens,* female, dorsum; *4, Metarhombognathus armatus,* deutonymph, dorsum; *5, Metarhombognathus armatus,* genital area of female showing perigenital and adanal setae; *6, Rhombognathus magnirostris,* female, venter; *7, Isobactrus setosus,* female, venter; *8, Rhombognathides pascens,* female, venter. Explanation of symbols in text.

caridae and is designated the preocular setae of the dorsal series (*ds-proc*). In *M. armatus* these lie between *AD* and *OC,* while in *Rhombognathides pascens* they are enclosed in *OC,* not only in the adults but in the deutonymphs and protonymphs as well. A second and third pair of setae can also be described with reference to the corneae, these being the laterocular (*ds-loc*) and postocular setae (*ds-poc*). In both forms these are within *OC* in adults as well as nymphs. The interocular setae (*ds-ioc*) lie posteriorly and medially of the preocular setae. The position of *ds-ioc* with respect to *PD* varies according to species and instar, being in *PD* in the adult of *Rhombognathides pascens,* but in the membranous area in the adult of *M. armatus americanus* and the deutonymphs of both species. Behind *ds-ioc* in

both species, are four additional pairs of setae, not including the adanal setae (*adans*). The position of these with respect to each other and to *PD* is also somewhat variable according to instar and species, but the number is always the same, and they can be readily homologized.

Turning now to *Rhombognathus notops* and *Isobactrus setosus*, we find a much different chaetotactic picture (Fig. 1, *1, 2*). *Ds-adp, ds-proc,* and *ds-ioc* are present, and can be recognized without question. In *R. notops*, both of the latter are found in *OC*, while in *I. setosus* both are in the membranous area. Moreover, *ds-proc* in *I. setosus* is extremely minute [2] and apparently absent in some individuals. But the alveolus is present even if the shaft is not. *Ds-loc* and *ds-poc* are both absent in these two species. In all species of *Rhombognathus* there are two or three refractile rings in the margin of *OC*, and two of these are in the position normally occupied by *ds-loc* and *ds-poc*. These are believed to be the vestiges of these setae. When a third ring is present, it lies between the vestiges of *ds-loc* and *ds-poc*. In *I. setosus, levis,* and *hutchinsoni*, only one ring is constantly present, and its position indicates that it is the vestige of *ds-poc* (Fig. 1, *1*). In some specimens of *I. setosus*, a second ring may be seen in the position of *ds-loc*. Setal vestiges in the form of residual alveolar rings are not common in the Acari, although they are of more frequent occurrence than generally realized.

In all species of *Rhombognathus* seen by the writer, there are either one or two pairs of setae behind *ds-ioc* and these are always in *PD*. Whether or not the four pairs of setae behind *ds-ioc* in *Rhombognathides* and *Metarhombognathus* represent a simple duplication of these setae cannot be ascertained on the basis of present evidence. In *Isobactrus* there may be two pairs of setae in *PD* (*I. setosus*), or one pair (*I. levis*), or none (*I. hutchinsoni*). The precise morphological relationship of each of these pairs of setae to those of the other three genera cannot be stated.

Anterior epimeral setae (*aes*). These show only one major modification in the Rhombognathinae. In *Rhombognathides pascens, Isobactrus setosus* and *Metarhombognathus armatus americanus* there are three and only three pairs of setae which lie in *AE* or the area normally occupied by *AE*. These are designated *aes-I, aes-II-lat* and *aes-II-v* (Fig. 1, *7, 8*). *Isobactrus* species have all of these outside the sclerotized remnants of *AE*, but in *Rhombognathides* and *Rhombognathus* they are always included within the plate. In *M. armatus americanus* the setae all lie in the margin of the sclerotized area although the alveoli of *aes-II-v* and *aes-II-lat* are virtually in contact with striated cuticle.

Rhombognathus notops and related species are exceptional in the family in that they have additional setae on *AE*. These may be designated the adjunctive setae of *AE* (*aes-II-adj*). They vary in number from one to three on each side, and their position is always lateral and dorsal to *aes-II-lat*.

Posterior epimeral setae (*pes*). The orthotrichous arrangement is found in *Metarhombognathus armatus americanus, Rhombognathides pascens,* and *Isobactrus setosus*. In all three there is a seta dorsolaterally (*pes-III-lat*), one anterior to the insertion of III (*pes-III-v*) and one anterior and somewhat medial to the insertion of IV (*pes-IV*). Neotrichy is found only in *Rhombognathus notops* and related species, in which there are two additional setae anterior to III (*pes-III-adj*).

Perigenital setae (*pgs*). Here the extreme neotrichy of the genital area in the male makes it difficult to use this group of setae systematically above the species level. Even this is not without exception, however, for in the genus *Rhombognathus*

[2] These setae were overlooked by the writer in his 1947 monograph, not only in *Isobactrus setosus*, but also in *I. hutchinsoni* Newell 1947 and *I. levis* (Viets) 1927. They are present in all three species, although very minute.

there are certain characteristic groupings of the perigenital setae of the male which are of supraspecific value. Thus, we find that in the male of *R. notops* and several related species the perigenital setae form a Λ-shaped configuration, inside the base of which is a single pair of basilar setae. In *R. peltatus,* and certain other species seen by the writer, there are two pairs of setae inside the base. The males of nearly all species in this genus fall into one or the other group. However, at least two species show arrangements which cannot be referred simply to either of these types.

The chaetotaxy in males of the other species of Rhombognathinae is more difficult to reduce to uniform types.

The perigenital setae in the females are generally more conservative. The chaetotaxy of the genital plate in *Rhombognathides pascens, Metarhombognathus armatus* and *Isobactrus setosus* may well be considered orthotrichous, all three species having three pairs of setae surrounding the genital opening. All other species in these three genera have three pairs of setae here, with the exception of *Metarhombognathus nudus* in which Viets showed the anterior pair of setae to be duplicated, making a total of four pairs of perigenital setae.

In *Rhombognathus* neotrichy is common, with the perigenital setae numbering one, two, three, four or five pairs. Only about six of the species (both described and undescribed) known to the writer have three pairs, one has only one pair, two have two pairs, four have four pairs, while the remainder have five pairs of perigenital setae in the female. Despite the high rate of interspecific variation, the number and disposition of the perigenital setae is very constant, being altered only by the expected occasional deletions and duplications, which are almost invariably unilateral. It is interesting to note in this connection that the frequency of individual variation in the number of setae is appreciably higher in *Rhombognathus* than in the Halacarinae, where interspecific variation in these setae is extremely rare in most genera. But the frequency is never high enough to impair the usefulness of the character at the species level.

Subgenital setae (*sgs*). The systematic significance of these setae has been all but ignored by previous workers in the Halacaridae, yet they are most useful morphological landmarks. The term subgenital setae is applied only to those external setae which are on the paired genital sclerites guarding the genital opening, or in a comparable position beside the unarmored genital opening. There are other setae also associated with the opening, but internal. These may be designated the *endogenital setae.* While they are doubtless important from a morphological standpoint, for several reasons they are difficult to study and have been quite generally overlooked.

As in the case of the perigenital setae, the subgenital setae of the female are less variable than those of the male. In *Rhombognathus notops* and all other species of this genus seen by the writer, there are two pairs of setae on the genital sclerites of the females (Fig. 1, *6*). In *Metarhombognathus armatus* and *M. nudus,* as well as in *Rhombognathides pascens* and its relatives, there are no subgenital setae whatever (Fig. 1, *5, 8*). In all species of *Isobactrus* seen by the writer, there is a single pair of setae here (Fig. 1, *7*).

Adanal setae (*adans*). These are among the most constant setae in the Halacaridae, almost ranking with the setae of *AD* in their constancy of occurrence. Therefore the absence of these setae in any species or group of species is noteworthy. In *Rhombognathus notops* these are borne dorsally on the anal papilla at the line of fusion between *PD* and *GA*. Their relationship to the anal plate is amply demonstrated by the numerous cases of forms in which *PD* and *GA* are separate. In these cases, the adanal setae are associated with *GA* rather than *PD*. Their position in *Rhombognathides pascens* is about the same as in *Rhombognathus notops,* but in the deutonymphs of *Metarhombognathus*

armatus these are visible only in ventral view. In *Isobactrus setosus, hutchinsoni,* and *levis* they are totally absent.

Female genital opening and genital sclerites. The genital opening is always guarded by a pair of genital sclerites. The most distinctive type is found in *Rhombognathides pascens, R. seahami, R. mucronatus,* and *R. merrimani* in which the sclerites are broad, heavy, and cusp-like, situated at the extreme posterior end of *GA*. They have no setal insertions. In *Rhombognathus notops* they are more elongate, not displaced so far posteriorly, and are not so thick-walled as in *Rhombognathides*. Moreover, they bear the two pairs of subgenital setae which have been found in all related species seen by the writer. They could scarcely be described as cusp-like despite the fact that in certain species they are bluntly pointed posteriorly. In a few species they are strap-like, of nearly uniform width throughout their length.

Isobactrus setosus, I. hutchinsoni, and *I. levis* have genital sclerites which are very feebly developed, elongate and strap-like. They bear a single pair of setae.[3] Generally two pairs of curved, dentate endogenital setae can be seen under the sclerites (Fig. 1, 7). Finally, in *Metarhombognathus armatus* and *M. nudus,* the two genital sclerites form an isosceles triangle, with the apex directed anteriorly. They are totally unlike the sclerites in any of the other species, and bear no setae.

Thus, the genital sclerites differ markedly in form and position, and furthermore in chaetotaxy, bearing 0, 1 or 2 pairs of setae.

Body armor. Outside of the several chaetotactic features that have been pointed out above in discussing the chaetotaxy of the body plates, there are a few other variants worthy of special note. One of these is the exceptional ontogenic characteristic found in *Metarhombognathus armatus* and *M. nudus*. In all Rhombognathinae except these two, the various plates comprising the body armor show a progressive increase in size as the individual passes through the protonymphal, deutonymphal, and adult stages. In the two species noted above, this same pattern is followed up to the deutonymph, which is heavily armored. But the adults which emerge from these deutonymphs are poorly armored, the plates being not just relatively but actually smaller than in the preceding instar. This is so unusual in the Acari that Viets was misled to describe the adult of *M. armatus* Lohmann (1893) as a new species, *Rhombognathopsis mollis* Viets 1927. A short time later he discovered a second species in material from the Murmansk coast, and described the adult as *Rhombognathopsis nudus* Viets 1928, the deutonymph as *Rhombognathopsis contectus* Viets 1928.

The anterior epimeral plate in *Rhombognathus notops* Gosse and *Rhombognathides pascens* is undivided medially as in the vast majority of Halacaridae. In fact, in the adults of some species of *Rhombognathus, AE* is largely or entirely fused with *PE* and *GA,* to form a solid ventral plate. Contrasted with this are *Isobactrus setosus* and *Metarhombognathus armatus* in which the right and left halves of *AE* in the adult are separated by membranous cuticle. In all species of *Isobactrus, aes-II-v* actually lie in the membranous area, while in *M. armatus* these lie within the very posterior angles of the right and left halves of *AE*. The most extreme reduction in *AE* is found in *I. levis* in which all three pairs of *aes* lie in the membranous area.

The bacillum and prebacillum of tarsus I. Despite the manifest disfavor with which Viets regards these structures, the writer regards them as among the most significant characters for demonstrating natural groups in the Rhombognathinae. In organisms whose body length rarely

[3] The author (1947, p. 72, Fig. 59) represented the subgenital setae by broken lines, suggesting that they were covered by the sclerites, like the endogenital setae. Study of more favorable material shows that these are actually external and are the true subgenital setae.

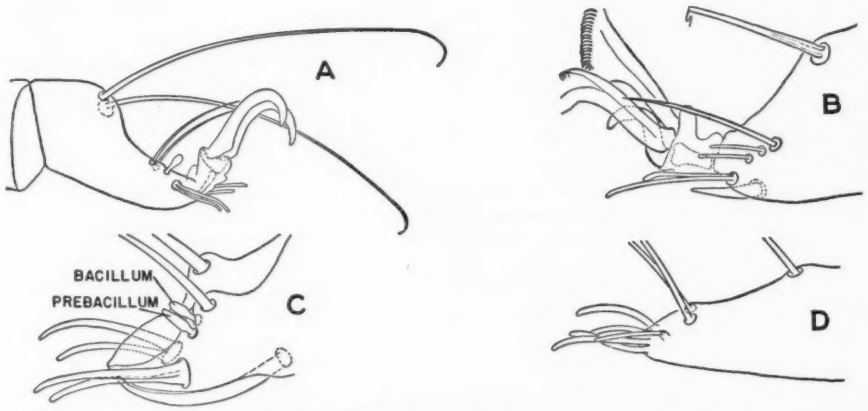

FIG. 2. Variation in prebacillum and bacillum in the four genera of the Rhombognathinae. *A, Isobactrus levis,* female, tarsus II; *B, Rhombognathides seahami,* male, tip of tarsus I; *C, Metarhombognathus armatus,* female, tip of tarsus I; *D, Rhombognathus magnirostris,* female, tip of tarsus I.

exceeds a half millimeter it is scarcely necessary to make apologies for giving serious consideration to some organs which occasionally require observation under oil immersion. The simplest arrangement of these setae is found in *Isobactrus* in which there is a single rod-shaped or clavate seta just distal to the lateral member of the distidorsal pair of setae (Fig. 2, *A*). In nearly all species of *Isobactrus* this is clavate in form, although in *I. setosus* it is best described as bacilliform.

In *Metarhombognathus armatus* the bacillum on I-6 is duplicated (Fig. 2, *C*), the additional member of the group being called the prebacillum. Both are well formed, clavate, but small. The situation in *M. nudus* is not ascertainable because of the inadequacy of the description of this species. In *Rhombognathides* there is also a bacillum and prebacillum on I-6, but these are relatively slender, being more than five times as long as thick (Fig. 2, *B*).[4]

The prebacillum in *Rhombognathus* species is well developed, while the bacillum is rudimentary and usually not even setiform (Fig. 2, *D*). But in one undescribed species seen by the writer, the bacillum is perfectly formed although only one-fourth as long as the prebacillum, showing beyond reasonable doubt that the vestigial structure in other species is indeed the bacillum. In all four genera there is only the bacillum on tarsus II.

Carpite. In the Halacarinae the tarsus ends in a relatively blunt point which provides an articulating surface for the middle piece of the ambulacrum. In the

[4] The writer wishes to correct the error made when it was reported that *Rhombognathides* species have only the bacillum on I-6 (Newell, 1947, p. 29, Figs. 23, 47). Although occasional specimens do have only one seta here a restudy of the dissection from which the earlier figure was drawn shows that it was drawn from tarsus II, and that tarsus I has a prebacillum in addition to the bacillum. Moreover, restudy of all forms in the author's collections from eastern North America and the British Isles shows that every adequately described species of *Rhombognathides* has this arrangement. Usually these two setae cannot be resolved because of the unfavorable position of the tarsus, or because they are so closely appressed to each other. But wherever the position of the tarsus is favorable (as in dissections), two setae can be seen. Only two cases were encountered in which there was only the bacillum, and these evidently involved deletions.

Rhombognathinae there is an additional sclerite, the carpite, between the tip of the tarsus and the ambulacrum, which appears to provide greater flexibility of the carpus. There are two distinct types of carpite in the Rhombognathinae. In *Rhombognathus notops, Metarhombognathus armatus,* and *Rhombognathides pascens* it is a solid, inflexible sclerite, attached either to the carpal membrane or, more likely, to the tip of the tarsus by an optically isotropic membrane (see Newell, 1947, pp. 43, 46, Fig. 11). In *I. setosus, I. hutchinsoni,* and related species, the tip of the tarsus continues imperceptibly into the carpite. The flexibility of the carpite, instead of being confined to the tarso-carpital and carpito-ambulacral joints as in the forms with a rigid carpite, is distributed throughout the length of the carpus. The tarso-carpital joint is absent.

Tarsal claws. The majority of species of Rhombognathinae have two claws on all tarsi. The form of these is quite variable, ranging from the smooth claws of *Isobactrus hutchinsoni, I. levis,* and *Rhombognathides merrimani* to the elaborately pectinate ones found on *Rhombognathides pascens* and *R. seahami.* The form of the claw has little systematic value above the species level.

There are three known arrangements in the number of claws on the tarsi. In *Rhombognathus notops* and *Isobactrus setosus* there are two claws on all tarsi (2-2-2-2), in *Rhombognathides pascens* there are three claws on I and II, but only two on III and IV (3-3-2-2), while in *Metarhombognathus armatus* there are three claws on all tarsi (3-3-3-3). Viets (1927) based his subdivision of the genus *Rhombognathus* on this variation in the number of claws, and indicated the following subgenotypes:

Other characters of supraspecific rank. The characters treated above by no means exhaust the list of those which have a bearing upon the taxonomy of this group, but they are the major ones and will be adequate for the purposes of this paper. Other characters include the occasional fusion of the dorsal plates, the form of the lateral claws, the parambulacral setae, and the chaetotaxy of basifemur II and patella III. These characters usually show a heterogeneous distribution, however, and clearly are not of generic import.

The variants discussed in detail above are summarized in the list given below, in order to permit a precise analysis of their distribution in the Rhombognathinae.

Summary List of Supraspecific Characters in the Rhombognathinae

1*a*. Dorsal setae of adults and nymphs numbering nine pairs, exclusive of the adanal setae.

1*b*. Dorsal setae of adults and nymphs numbering not more than five pairs.

2*a*. *Ds-proc* in *OC*.

2*b*. *Ds-proc* in membranous area between *AD* and *OC*, occasionally rudimentary, with only the alveolus present.

3*a*. *Ds-loc* and *ds-poc* present.

3*b*. *Ds-loc* and *ds-poc* absent, represented at most by cuticular rings (vestigial alveoli) completely devoid of shafts.

4*a*. *AE* with only three pairs of setae, *aes-I, aes-II-lat* and *aes-II-v*.

4*b*. *AE* with one to three pairs of adjunctive setae (*aes-II-adj*) lateral and dorsal to *aes-II-lat*.

5*a*. *AE* in adults divided medially, right and left halves separated by striated membranous cuticle extending to the base of the gnathosoma and with at least *aes-II-v* in membranous area.

5*b*. *AE* in adults not divided medially; *aes-II-v* in the plate.

6*a*. *PE* with adjunctive setae (*pes-III-adj*) dorsolaterally near insertion of III, in addition to *pes-III-v, pes-III-lat,* and *pes-IV*.

Subgenus	Subgenotype	Claw Type
Rhombognathus s. str.	*Pachygnathus notops* (Gosse) 1855	2-2-2-2
Rhombognathides Viets 1927	*Aletes pascens* (Lohmann) 1889	3-3-2-2
Rhombognathopsis Viets 1927	*Pachygnathus seahami* (Hodge) 1860	3-3-3-3

6*b*. *PE* with only *pes-III-v, pes-III-lat,* and *pes-IV; pes-III-adj* absent.

7*a*. Female with two pairs of subgenital setae on the genital sclerites.
7*b*. Female without subgenital setae.
7*c*. Female with one pair of subgenital setae.

8*a*. Male with two or sometimes one pair of subgenital setae.
8*b*. Male with four pairs of subgenital setae.

9*a*. Adanal setae present.
9*b*. Adanal setae absent.

10*a*. Female genital sclerites cusp-like, displaced to posterior end of body, or entirely concealing the anus in ventral view.
10*b*. Female genital sclerites not cusp-like but more elongate, band-like, not concealing the anus in ventral view.

11*a*. Deutonymphal armor not as heavy as that of adults, the plates not only relatively but actually smaller than in the adult.
11*b*. Deutonymphal armor heavier than that of adults, the plates both relatively and actually larger than in the adults.

12*a*. Tarsus I with bacillum only.
12*b*. Tarsus I with bacillum and prebacillum, both of which are short, less than five times as long as thick.
12*c*. Tarsus I with prebacillum long, bacillum less than one-third as long as prebacillum, and most often rudimentary.
12*d*. Tarsus I with both bacillum and prebacillum relatively long, slender, more than five times as long as thick.

13*a*. Carpite a rigid sclerite, appearing distinct from tarsus, although joined to end of tarsus by soft, flexible chitin.
13*b*. Carpite flexible throughout length, joined imperceptibly to end of tarsus.

14*a*. With two claws on all tarsi (2-2-2-2).
14*b*. With three claws on all tarsi (3-3-3-3).
14*c*. With three claws on I and II, two on III and IV (3-3-2-2).

Distribution of Variants

Here, two additional terms will be defined. *Harmonious distribution of variants* or *harmony* is that condition in which all species of a genus (or members of a group at any level) have the same expression of the character, i.e., exhibit the same variant of a given character. For example, all species of *Rhombognathides* lack subgenital setae. *Concomitance* is that condition in which all species of a given genus show harmony in two or more character variants. For example, all species of *Rhombognathides* (1) lack subgenital setae, (2) have cusp-like genital sclerites in the female, and (3) have a bacillum and prebacillum on tarsus I. The distribution of the variants treated above will now be analyzed. First, the species will be listed according to the writer's system (Table I) and then according to Viets' system (Table II). In Table II, the writer has arranged the species under the subgeneric categories into which they fall on the basis of their claw formulae, but has still retained the generic names recognized by him. As explained before, this is done to prevent nomenclatorial confusion, at the risk of some initial confusion to the reader. Along the top of the table, the numbers correspond to those in the summary list of supraspecific characters, while the letters show which particular variant of the character is found in each species. Since most of the adequate descriptions of species of *Rhombognathus* are still in manuscript form, it is necessary to list these *en masse*. However, they show no deviations whatever from the same basic pattern, and all nine have precisely the same formula for all characters.

The tables are based on eleven forms of *Rhombognathus,* six of *Rhombognathides,* two of *Metarhombognathus,* and seven of *Isobactrus.* The list of species is, therefore, not a selected one, the only criterion for exclusion of a form being the lack of an adequate description.

The columns in Table I should be read vertically. An examination of the table shows that not until we introduce character 14 (number of claws) do we encounter anything but complete harmony in the distribution of the variants within the different genera. Only one case is found (*Rhombognathides* 14, *abc*) in which all three claw arrangements occur within the genus. The remaining 55 possibilities show complete harmony (55/56= 98 per cent). Turning now to Table II, we see a much different picture. The subgenus *Rhombognathides* as defined by

TABLE I—ARRANGEMENT OF SPECIES, AND DISTRIBUTION OF CHARACTERS IN ADULTS OF THE RHOMBOGNATHINAE ACCORDING TO AUTHOR'S SYSTEM

GENUS	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Rhombognathus Trt.														
magnirostris	b	a	b	b	b	a	a	a	a	b	a	c	a	a
spp. (9 undescribed)....	b	a	b	b	b	a	a	a	a	b	a	c	a	a
notops	b	a	b	b	b	a	a	a	a	b	a	c	a	a
Isobactrus Newell														
setosus	b	b	b	a	a	b	c	b	b	b	a	a	b	a
hutchinsoni	b	b	b	a	a	b	c	b	b	b	a	a	b	a
levis	b	b	b	a	a	b	c	b	b	b	a	a	b	a
*uniscutatus**	b	b	b	a	a	b	c	b	b	b	a	a	b	a
magnus	b	b	b	a	a	b	c	b	b	b	a	a	b	a
spp. (2 undescribed)....	b	b	b	a	a	b	c	b	b	b	a	a	b	a
Rhombognathides Viets														
pascens	a	a	a	a	b	b	b	a	a	a	a	d	a	*c*
scahami	a	a	a	a	b	b	b	a	a	a	a	d	a	*b*
merrimani var. *m*.....	a	a	a	a	b	b	b	a	a	a	a	d	a	*a*
m. var. *needleri*.....	a	a	a	a	b	b	b	a	a	a	a	d	a	*c*
mucronatus	a	a	a	a	b	b	b	a	a	a	a	d	a	*b*
*spinipes**	a	a	a	a	b	b	b	?	a	a	a	d	a	*a*
Metarhombognathus Newell														
armatus	a	b	a	a	a	b	b	a	a	b	b	b	a	b
nudus	a	b	a	a	a	b	b	?	a	b	b	b	a	b
SUMMARY														
Rhombognathus	b	a	b	b	b	a	a	a	a	b	a	c	a	a
Isobactrus	b	b	b	a	a	b	c	b	b	b	a	a	b	a
Rhombognathides	a	a	a	a	b	b	b	a	a	a	a	d	a	*abc*
Metarhombognathus	a	b	a	a	a	b	b	a	a	b	b	b	a	b

* In his earlier paper the author (1947, p. 28) because of uncertainty about their true position, left *Rhombognathus uniscutatus* Viets 1939 and *Rhombognathus spinipes* Viets 1933 in the genus to which they were assigned originally. It was pointed out, however, that neither one belonged in the genus. Subsequently, Viets has kindly sent the writer specimens of *R. uniscutatus* and Willmann (1952, pp. 166–167) has described the adult of *R. spinipes*. These species can now be placed in their proper respective genera, *Isobactrus* and *Rhombognathides*.

Viets exhibits no disharmony in any of the character groups (there are only two species, the others being distributed by Viets in the subgenera *Rhombognathus* and *Rhombognathopsis*). But harmony is much less marked in *Rhombognathopsis*, being found in only nine of the fourteen characters. And in *Rhombognathus* the situation is almost totally chaotic, with only two of the fourteen character groups showing a completely harmonious distribution throughout all species. An analysis of Table II reveals only 25 out of 42 possible cases of harmonious distribution of characters (60 per cent). If we omit character group 14, which is the principal one in question, then Table I shows 100 per cent harmonious distribution, while Table II shows only 54 per cent harmonious distribution of the thirteen other variants.

The tables can be summarized in another way which provides an analysis of significance. If we tabulate the number of variants in which each genus differs consistently from the others, we find these results:

From Table I (author's concept of the genera):

Rhombognathus differs consistently from *Rhombognathides* in 7 out of 14 characters.

Rhombognathus differs consistently from *Metarhombognathus* in 10 out of 14 characters.

Rhombognathus differs consistently from *Isobactrus* in 9 out of 14 characters.

Rhombognathides differs consistently from *Metarhombognathus* in 5 out of 14 characters.

Rhombognathides differs consistently from *Isobactrus* in 10 out of 14 characters.

Metarhombognathus differs consistently from *Isobactrus* in 9 out of 14 characters.

From Table II (Viets' concept of the subgenera):

Rhombognathus differs consistently from *Rhombognathides* in 1 out of 14 characters.

TABLE II—ARRANGEMENT OF SPECIES, AND DISTRIBUTION OF CHARACTERS IN ADULTS OF RHOMBOGNATHINAE ACCORDING TO VIETS' SYSTEM

SUBGENUS	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Rhombognathus (s.s.)														
Rhombognathus magnir..	b	a	b	b	b	a	a	a	a	b	a	c	a	a
spp. (9 undescribed)....	b	a	b	b	b	a	a	a	a	b	a	c	a	a
Rh. notops.....	b	a	b	b	b	a	a	a	a	b	a	c	a	a
Rh'ides. merrimani m...	a	a	a	a	b	b	b	a	a	a	a	d	a	a
Rh'ides. spinipes.....	a	a	a	a	b	b	b	?	a	a	a	d	a	a
I. setosus.....	b	b	b	a	a	b	c	b	b	b	a	a	b	a
I. hutchinsoni.....	b	b	b	a	a	b	c	b	b	b	a	a	b	a
I. levis.....	b	b	b	a	a	b	c	b	b	b	a	a	b	a
I. uniscutatus.....	b	b	b	a	a	b	c	b	b	b	a	a	b	a
Rhombognathides														
Rh'ides pascens.....	a	a	a	a	b	b	b	a	a	a	a	d	a	c
Rh'ides merrimani n.....	a	a	a	a	b	b	b	a	a	a	a	d	a	c
Rhombognathopsis														
Rh'ides seahami.....	a	a	a	a	b	b	b	a	a	a	a	d	a	b
Rh'ides mucronatus.....	a	a	a	a	b	b	b	a	a	a	a	d	a	b
M. armatus.....	a	b	a	a	a	b	b	a	a	b	b	b	a	b
M. nudus.....	a	b	a	a	a	b	b	?	a	b	b	b	a	b
SUMMARY														
Rhombognathus	ab	ab	ab	ab	ab	ab	abc	ab	ab	ab	a	acd	ab	a
Rhombognathides	a	a	a	a	b	b	b	a	a	a	a	d	a	c
Rhombognathopsis	a	ab	a	a	ab	b	b	a	a	ab	ab	abd	a	b

Binomials are those recognized by writer, not Viets. See text for explanation.

Rhombognathus differs consistently from *Rhombognathopsis* in 1 out of 14 characters.
Rhombognathides differs consistently from *Rhombognathopsis* in 1 out of 14 characters.

Following the author's classification, and using all 14 character groups, each genus differs consistently from all others in a minimum of five and a maximum of ten out of fourteen characters (total, 50 out of a possible 84=60 per cent). Using Viets' classification, each subgenus differs consistently from the others in only a single character (total, 3 out of a possible 42=7 per cent). If we eliminate the main character in question (number 14), then the writer's system shows consistent differences in 48 out of a possible 78 cases, or 62 per cent, while Viets' system shows no consistent differences whatever in 39 possible cases! In the light of this simple analytical approach to the problem of deciding which of two systems of classification is the more natural, Viets would have done well indeed to reconsider his claim that it is the author's system which is "nicht hinreichend begründet."

It is clear from these figures that Viets made the unfortunate initial mistake of selecting a character which, while convenient to use, was one with a high degree of variability in *Rhombognathides*. In this genus, not only do we find the 3-3-2-2 claw formula, but the two other formulae found in the other genera as well. This situation, while apparently unique in the Trombidiformes, certainly does occur in other groups of the Acari. In many genera of the Oribatei, the number of claws is a character of only specific value. In fact, Willmann (1931, pp. 271–272) has reported mono-, di-, and tridactyl varieties within a single species (*Scheloribates praeincisus* Berlese 1910), somewhat as in the case of *Rhombognathides merrimani*.

The classification proposed by the writer in 1947 was based on sound morphological grounds, in strict accordance with the international rules of nomenclature, and must stand. It is summarized as follows:

Rhombognathus Trouessart 1888 (= *Aletes* Lohmann 1889)

Rhombognathides Viets 1927 (= *Rhombognathopsis* Viets 1927)[5]

[5] Viets designated as types of *Rhombognathides* and *Rhombognathopsis* two sibling

Metarhombognathus Newell 1947
Isobactrus Newell 1947

Criteria for Evaluating Significance of Variants

While the above procedure is valuable in detecting species groups, it must be used with discretion, and in the final analysis the naturalness of any system is limited by the judgment of the systematist. It is especially important to select carefully the variants to be used, and here it might be well to set down a few criteria which should be kept in mind when distinguishing between variants of specific and generic importance.

Uniqueness. At the generic level, the systematic significance of a character variant is determined by two criteria above all others: (1) the consistency with which the character is distributed throughout the members of the genus, and (2) the uniqueness of the character. A number of the variants noted above are unique to one of the four genera, namely:

Rhombognathus—4*b*, 6*a*, 7*a*, 12*c*
Isobactrus—7*c*, 8*b*, 9*b*, 12*a*, 13*b*
Metarhombognathus—11*b*, 12*b*
Rhombognathides—10*a*, 12*d*, 14*c*

The latter variant, while unique to *Rhombognathides*, is not the only one, for all three claw formulae are found in this genus. But until further study proves otherwise, the possession of any one of these variants by any given species is *prima facie* evidence that the species belongs to the genus in question.

Concomitance. However, uniqueness is not absolutely essential. In some cases, certain combinations of characters showing a mutually exclusive distribution of the variants in closely related species groups may have generic significance. For example, if we take the first three of the characters in the foregoing list, we find that the variants have the following distribution:

	1	2	3
Rhombognathus	b	a	b
Isobactrus	b	b	b
Rhombognathides	a	a	a
Metarhombognathus	a	b	a

While the number of dorsal setae clearly sets off all species of *Rhombognathides* and *Metarhombognathus* from all other species of Rhombognathinae, this character is of no value in separating *Rhombognathides* from *Metarhombognathus*, or *Rhombognathus* from *Isobactrus*. Turning to the second character, we find that *ds-proc* lies in the ocular plate in *Rhombognathus* and *Rhombognathides* but in the membranous area in *Isobactrus* and *Metarhombognathus*. The separation of the Rhombognathinae into four species groups on the basis of two characters is thereby complete. None of the six variants noted above is unique to any one group, but each combination of variants is found in only one.

While it is likely that some groups of natural genera can be differentiated solely on the basis of combinations of non-unique variants, the inclusion of one or more harmoniously distributed singular variants always lends conviction to the system.

Radicalism. One manifestation of uniqueness and at times inseparable from it is *radicalism*. The term is used antithetically to *conservatism* to denote unusual variants in characters which are otherwise totally constant. By contrast, a unique variant may be found in a character which shows little intergeneric stability. One excellent example of radicalism treated above is the absence of the adanal setae in *Isobactrus*. There is perhaps no group of species in the entire family Halacaridae in which these are absent except for those centering around *I. setosus*. In this case, the variant is both unique and radical, but it is entirely possible that some radical characters might be shared by two genera. Characters of this kind usually have generic import, but not

species which are necessarily congeneric. Had he used *Rhombognathus armatus* Lohmann 1893, then *Rhombognathopsis* would still stand. But he did not, and *Rhombognathopsis* therefore is not available. *Rhombognathides* had line priority over the other name.

always. An example from the genus *Copidognathus* is worthy of note in this connection. In this genus, easily one of the largest in all the Acari, the setae of the anterodorsal plate nearly always lie in front of the porose area or areas, or else in front of the position these areas would normally occupy. But in *C. tricorneata* Lohmann 1938, *C. hummelincki* (Viets) 1936, *C. adriatica* (Viets) 1940, *C. kagamili* Newell 1949, and *C. caudatus* Newell 1947, these lie posterior to the porose area. Yet there is not one other known character possessed by these species which would set them off from the others; moreover, *C. caudatus* does not appear to be very closely related to the other four, which do form a natural group. Since they are otherwise typical *Copidognathus* species, there is no reason to set them apart from the rest of the genus. Hence, even radical characters must be used with discretion, and here again, concomitance or lack of it, is the most reliable final criterion on which to base a decision as to the significance of radicalism in any given case.

Genetic and morphogenetic complexity within a single character. This is an important criterion, but one which is virtually impossible to measure. Yet it is certain that characters differ greatly in their morphogenetic complexity. One seemingly simple type of variation in mites involves the duplication, loss, or displacement of a particular pair of setae. But even here it is patent that the frequency of variations of this type within a particular group differs greatly, with some setae being more constant in position and occurrence than others. Frequently individual pairs of setae are more constant than structures involving a considerably greater number of cells. Again we can cite the adanal setae of the Halacaridae as an example. Variations in these simple structures are far more exceptional than variations in the extent of the plates in the body armor, the form of the ovipositor, and the paneling of the plates, all of which involve much larger numbers of cells, sometimes in widely scattered parts of the body.

The same is true of many other setae, in particular those of the dorsal series and of the anterior and posterior epimeral series. The frequency of variation in the number of these is much lower than the frequency of variation in body size, or proportions of leg and palpal segments. It would seem that the genetic and morphogenetic systems controlling the development of these organs are in a sense more complex, or at least more immutable than those involved in the formation of larger structures. It is impossible to generalize that chaetotactic characters are more constant than others, however, for the great variability in the perigenital setae would invalidate such a generalization.

From these considerations it should be evident that morphogenetic complexity within a single character cannot be judged on the basis of number of cells involved and that it lies below the structural level at which systematists normally are compelled to work.

Morphogenetic complexity involving multiple characters (morphogenetic linkage or concomitance). It is certain, however, that morphogenetic complexity and concomitance are closely related, and roughly proportional. From the list of 14 characters showing supraspecific variations in the Rhombognathinae, there is only one instance in any of the four genera in which complete concomitance is lacking, and that is in the case of the tarsal claws in *Rhombognathides*. It is difficult to avoid the assumption that agreement in such a large number of characters implies a much more complex interrelationship of morphogenetic processes than would be required to produce concomitance in only two or three characters. To this extent concomitance may be considered a partial measure of morphogenetic complexity. Judging from the fact that the morphogenesis of many organs is linked, concomitance itself may be nothing more than the phenotypic expression of genetic link-

age. If this is so, then it may be stated that genera, as we know them today, owe their existence to genetic linkage.

Distribution of character variants in sibling species and varieties. It is well known that a character which shows no normal variation whatever in one genus is sometimes extremely capricious in another, appearing in two or more variant forms. In the one case, the character has generic significance; in the other it has none whatever, although it may provide useful specific characters. This is one of the more common sources of differing opinions on classification, particularly at the generic level.

One of the best checks that can be used in a dilemma of this type is that provided by sibling species and varieties. In the Rhombognathinae, one of the outstanding examples of sibling species is that of *Rhombognathides pascens* and *Rhombognathides seahami.* If one were to remove the claws from a large female of *R. pascens* and a small female of *R. seahami,* they could not be separated with any certainty whatever on the basis of existing descriptions, figures or keys.[6] Although the two species can be readily separated on the one character of the median claw, they satisfy fully the concept of sibling species. Accordingly, it is not logical to place them in different genera or subgenera, especially when in doing so one of them acquires such a strange bedfellow as *Metarhombognathus armatus.* Any morphological character which results in separating the members of a sibling pair of species is immediately revealed as having no generic or subgeneric import whatever in the species group involved.

Much the same can be said for varieties of a single species. *Rhombognathides merrimani,* known at present only from the New Brunswick coast of Canada, is represented by two readily differentiated forms. While it is not beyond the realm of possibility that these comprise another pair of sibling species, indications are that they are truly varieties.[7] One of these has

[6] Viets (1950, p. 19) criticized the writer's use of "the extremely close similarity" between *R. pascens* and *R. seahami* as evidence for the necessity of revising the old collective genus *Rhombognathus,* and went on to conclude "eine Begrundung der 'similarity' gibt Newell nicht weiter." On the contrary, several allusions to the similarity of the two species were made by the writer. It was pointed out (Newell 1947, p. 54) that Lohmann's (1889) "figs. 64 and 88 could very well represent the same species showing that Lohmann's specimens of *R. pascens* and *R. seahami* were as similar in dorsal view as those seen by the writer in North America. As pointed out above, a drawing of either species in dorsal view would serve for the other as well." The writer (1947, p. 51) stated of *R. seahami*: "Noticeably larger than *R. pascens,* but identical in form. Form of dorsal plates, chaetotaxy and sculpturing as in *R. pascens* so that Fig. 12 (*pascens*) will also serve for the recognition of this species." These were not idle words. Plate for plate, segment for segment, seta for seta, palp for palp, these are morphologically the same *except* for the claws and certain differences in the male genital area. They are truly sibling species.

Viets' criticisms contained other misleading or confusing statements that will be readily apparent to any one working in the group. However, these will not be discussed further, since this paper is primarily a treatment of systematic principles and procedures as exemplified by a study of the natural classification of the Rhombognathinae. Only one additional point will be mentioned here, as it involves an oversight on the part of the author. At the time of writing the monograph on the Halacaridae of eastern North America, I had overlooked Viets' correction (1936) of Schulz's misidentification of a specimen of *Rhombognathides mucronatus* as *Rhombognathides pascens.* With the clarification of this point, the writer is more than willing to accept Viets' statement that Schulz's observation was based on an erroneous determination.

[7] Viets pointed out that my Figures 30 and 31 (Newell, 1947) were evidently reversed, which is correct, for these should be interchanged to agree with the keys on pages 31 and 47, and the text on page 56. At the bottom of page 57, the writer inadvertently described *R. merrimani merrimani* as having a median claw on legs I and II. However, this came about, it was certainly my intent that the name *R. merrimani merrimani* be applied to the 2-2-2-2 variety and the name *R. merrimani needleri* to the 3-3-2-2 variety. This was

two claws on all tarsi as in *Rhombognathus,* while the other has a 3-3-2-2 claw formula as in certain *Rhombognathides* species. It is unthinkable that varieties of a single species could occupy different genera or even subgenera, but this would be necessary in order to preserve the old system of classification. Viets' suggested alternative to this, namely that the 2-2-2-2 variety represented an abnormality, is equally untenable. There are no intermediates and no unilateral variations; all individuals fall into either the 3-3-2-2 or the 2-2-2-2 type; and the writer has seen numerous individuals of both types. Abnormalities never exhibit this type of distribution.

Therefore, the invalidity of the claw formula as a primary or sole character upon which to base a division of the Rhombognathinae is clearly shown by a study of only four forms. Two of these comprise a pair of sibling species and the others a pair of varieties. According to the previous classification, they would be distributed as follows:

Rhombognathus (*sensu* Viets) 2-2-2-2	*Rhombognathides* (*sensu* Viets) 3-3-2-2	*Rhombognathopsis* Viets 3-3-3-3
Rhombognathides merrimani var. *merrimani*	*Rhombognathides merrimani* var. *needleri*	
	Rhombognathides pascens	*Rhombognathides seahami*

If there were rules of procedure in systematics, one of these would surely be that members of groups of sibling species, or varieties of a single species shall not be placed in different genera or subgenera. The above examples should illustrate the use of sibling species and varieties in evaluating the significance of certain character variants.

the author's first (and probably last) venture in variety naming. While the study and description of variation is most important in systematics, the naming of varieties is an endless and quite meaningless procedure. The writer's primary purpose in naming the two forms of *R. merrimani* was to focus attention on the untenability of any system which would result in placing two varieties of one species in different subgenera.

Conclusion

The author has generally followed two working principles in evaluating genera in the Acari which will render far more justice than injustice to the systematics of that and many other groups. The first is that if a group of species appears to represent a new genus, each member of the group will differ consistently in at least two, and usually more, significant characters from all species of the most closely related genus. If they do not meet this test, they are regarded as not constituting a separate genus. The second principle is that any established genus differentiated on a single character from its nearest relative is probably false, or if not false, then further search should reveal differences overlooked by the author of the genus. In addition to these two working principles, the writer has found within the field of his experience in the Acari that the erection of subgenera has little value. Certainly the majority of subgenera with which I am familiar have little or no biological meaning, if they are not actually misleading. The practice of establishing subgenera on single, "convenient" characters is deplorable, for a high percentage of these are fictitious, splitting closely related species into groups whose individual systematic homogeneity is no greater than that of the genus as a whole. "Convenience" is one of the poorest possible, and most commonly cited, excuses for establishing a new systematic group. Subgenera, like genera, must be natural groups, with their foundations on sound morphological, ecological, and distributional grounds, all members of the subgenus being more closely related to each other than to species outside. Since concomitance of two or more character vari-

ants is the best criterion for judging morphological and therefore systematic relationships, the writer feels that it is very rarely that a subgenus could be safely erected without such concomitance. If complete association between two or more pairs of differentiating characters is found, the writer would feel justified in most cases in erecting a new genus rather than a subgenus (working rule number one). Concomitance cannot be measured in the case of monospecific genera, of course, and here the ability of the observer to evaluate the significance of the observed differences is of paramount importance. The differences would necessarily be large. The guiding questions should always be: (1) does the change result in a forceful divorcement of naturally related forms? (2) is it more important to point out the differences involved in the case than to express relationship? (3) does the inclusion of one or more new species within an established genus result in the production of strange bedfellows?

These cannot be formulated into rigid procedural rules, of course, for systematics has too many facets and ramifications to be regulated by rules. This is one of the significant differences between nomenclature and systematics. It is necessary, however, that the worker who would call himself a systematist adhere as closely as possible to these principles, for they are the ones which make the difference between the systematist and the "nomologist." One thing above all should be kept in mind: systematics is essentially an attempt to interpret the course of evolution. The models used in this interpretation are borrowed from, and sometimes in return supplement the fields of morphology, cytogenetics, physiology, ecology, mathematics, and logic. The success with which these models are integrated and applied to systematic problems determines the quality of the system. The better the system, the more natural it will be, the more accurately it will depict natural relationships between species and between genera. The same principles can be projected into higher categories as well.

Summary

The systematic history of the Rhombognathinae is outlined briefly and the two conflicting concepts of the composition of the group are presented.

The characters of supraspecific significance, and the variants of these which are found in the Rhombognathinae are described. The distribution of these variants is then analyzed, with the species arranged first according to one system, and then the other.

With the species arranged according to the newer classification, harmonious distribution of the variants within the different genera is found in 55 out of 56 possible cases (98 per cent). With the species arranged according to the older system, harmony is found in only 25 out of 42 possible cases (60 per cent). Eliminating the character of the claw formula, these values become 100 and 54 per cent respectively.

Following the newer classification and eliminating the character of the claw formula, consistent intergeneric differences in distribution of the thirteen other groups of variants was found in 47 out of 78 possible cases (60 per cent), while the older system showed no consistent differences whatever in 39 possible cases.

The analysis revealed that Viets' system was faulty because it was based on a single character with a high degree of instability within one genus (*Rhombognathides*).

A number of criteria which should be considered in evaluating the systematic significance of character variants are discussed. These are (1) uniqueness, (2) radicalism, (3) morphogenetic complexity, (4) morphogenetic linkage (concomitance), (5) distribution of character variants in sibling species and varieties. Certain working principles found by the author to be of value in dealing with the systematics of the Acari are presented.

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Genera and Subgenera

The employment of subgenera has recently been a matter of some controversy, many workers advocating that they should either be suppressed or raised to the rank of genera. I remain in favour of their retention on the following grounds: (1) I consider that the two essential criteria of a genus are that it should be a natural assemblage of related species and that it should be clearly delimitable from other genera in all parts of the world—not necessarily or even preferably by a single character, but by some combination of characters. The latter criterion may and often does imply that a genus may include hundreds or even thousands of species. (2) In the case of large genera some species must obviously be more nearly related than others, and in local faunas these species-groups may be quite as clear cut as those forming other genera. This has often resulted in generic names being proposed for such groups, and these names may be much better known than those of the larger genera in which they have later been merged. In such cases it may be both convenient and advantageous to retain the older names as subgenera for use when desired. (3) The attempt to segregate and name all the species-groups in a large and complex assemblage merely results in a recurring cycle of inflation of the nomenclatorial currency and leads to utter confusion and breakdown of the system, besides tending to encourage superficial and unscientific studies; but there are advantages in using names for at least the primary divisions (subgenera) of a large genus and perhaps some alphabetical or numerical system, or the names of representative species, for the subdivisions. (4) Nevertheless the delimitation of genera will probably always involve some element of personality, and one worker will see a clearly-defined genus where another will not. The use of subgenera appears to me the simplest device for minimising the effect of this unavoidable personal element, as if the validity of subgenera be admitted the non-specialist can cite an insect by its generic name only while a specialist can equally correctly use the subgeneric name with or without that of the genus. (5) The adoption of comprehensive genera will eliminate the confusion liable to be caused by the duplication of specific names within a small group, a practice which is theoretically permissible if the elements in the group are treated as genera.

F. W. EDWARDS

The above statement is an excerpt from an unpublished manuscript left by Dr. Edwards, a distinguished dipterist and Deputy Keeper of Entomology, British Museum (Natural History), who died on Nov. 15, 1940. Quoted unchanged through the kind permission of the Trustees of the British Museum (Natural History).

An Objective Aid in Determining Generic Limits

MAURICE T. JAMES

THE present paper does not attempt to define a genus; it deals with the methodology rather than the philosophy of systematics. The genus, however, is here considered as a natural grouping of species, a branch of the phylogenetic tree. As such, its members have in common a number of fundamental characters, morphological and otherwise. The genus, therefore, is to be defined on the basis of the *totality* of characters, not on key characters which, though often fundamentally important, are primarily of utilitarian value. The method proposed here, one which I have used successfully, may avoid the creation of useless new generic names or concepts, many of which are proposed simply because they are based on forms which do not fit into existing keys. The method is not wholly original; Forbes (1934) used a similar plan in determining relationships between genera of the agrotine moths. The application to the differences existing within rather than among

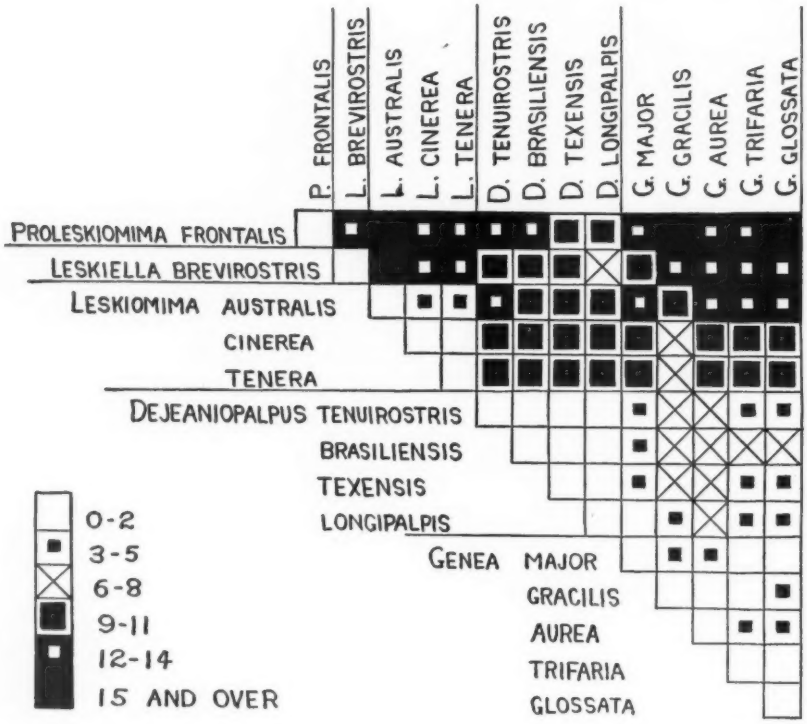

FIG. 1. Graphical presentation of differences existing between species and genera of Leskiini with the setulose first vein. For explanation, see text.

genera, however, appears to be a new one.

My review (James, 1947) of the larvaevorid tribe Leskiini was developed, first, by a study of all apparently significant morphological characters of the individual species, then by the determination of generic characters through a consideration of what apparently related species had in common. Only morphological characters could be used, since other information was too scant or unavailable. The study resulted in the grouping of the fourteen species into five genera, two of which were monobasic.

In order to apply the proposed method to the grouping of species into the leskiine genera, arbitrary values were used to evaluate variation in each of the characters, and the differences between species determined on this basis. For example, palpi may be short (1), medium (2), or long (3). The arbitrary values are given in parentheses. It is immaterial, for the purposes of this paper, how "short," "medium," and "long" are defined, but, obviously, some objective standard should be used in determining this. *Leskiomima tenera* and *L. australis* have short palpi, *Genea aurea* medium, and *G. trifaria* long. Therefore, the differences with regard to this character between *L. tenera* and *L. australis, G. aurea* and *G. trifaria,* are, respectively, 1−1=0, 2−1=1, and 3−1=2. By assigning similar values to other characters, and adding results, we obtain the totals of all differences between any two species. For example, *L. tenera* differs from *L. australis, G. aurea,* and *G. trifaria* by a total of 3, 10, and 10, respectively.

The results are shown graphically in Figure 1. The two monobasic genera stand out clearly as distinct from each other and from each of the other three genera. *Dejeaniopalpus* appears to be quite homogeneous; *Leskiomima* and *Genea* appear fairly so, the greatest difference values being in the 3–5 class (actually, 3 and 4, respectively). *Leskiomima* stands out very distinctly from *Dejeaniopalpus* and *Genea,* but the relationship of the latter two to each other is quite obvious; probably they should be considered subgenera.

The method proposed is independent of the problem of lumping and splitting. It defines groups of species which are set apart from other groups; to an extent, it defines the gaps existing between pairs of related groups. It cannot substitute for the good judgment of the experienced taxonomist; it may merely be an aid to him and a still more valuable one to the beginner. It attempts to make judgments more nearly objective. It can neither evaluate the importance of individual characters nor dictate what elements are to be united. It indicates the peaks and valleys, and leaves to the judgment of the systematist the problem of delimiting the major ranges and plateaus.

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Species Differences in Amino Acids of *Culex* Mosquitoes

GORDON H. BALL and EDGAR W. CLARK

IF ONE considers the criteria used for the determination of specific differences among more or less closely related plants or animals, it will be noted that, except for studies on various micro-organisms, those tests based upon comparative physiology or comparative biochemistry have not been widely used.

With the introduction of techniques for the detection, with a high degree of accuracy, of minute amounts of the more complex and supposedly more "specific" components of the bodies of organisms, the possibilities are greatly enhanced for demonstrating biochemical differences between higher plants or animals of very similar morphology. Among the more reliable and reproducible techniques are those of microbiological assay, microelectrophoresis, and paper chromatography. Paper chromatography is particularly valuable in the determination of amino acids, since quantitative concentrations as low as a fraction of a microgram can be detected (Pratt and Auclair, 1948), while qualitative determinations can be made easily by using known amino acids as references.

Insects are especially useful in amino acid determinations, since they show a particularly high concentration in their blood compared with that found in other animals (Pratt, 1950). Various workers have identified the amino acids found in insect tissues, but apparently only Micks and Ellis (1951, 1952) and Clark and Ball (1951, 1952) have attempted to compare the pictures obtained from species which are at present commonly recognized as being within a single genus.

Among investigations of higher organisms, there seem to have been, previous to the work referred to above, no reports of the use of an entire plant or animal. Work using only a part of an organism, e.g., the comparison of the amino acids found in muscle tissues of different animals used as food, shows some differences, both qualitative and quantitative, between more widely separated groups and indicates in addition that the amounts and/or kinds of amino acids may vary from tissue to tissue in a single organism (Beach, Munks and Robinson, 1943; Block and Mitchell, 1946).

Quantitative differences in amino acid concentration have been reported between insects of different families (Duchâteau, Sarlet and Florkin, 1952) and of different genera (Micks and Ellis, 1951). And recently, in a preliminary communication, Buzzati-Traverso and Rechnitzer (1953) have noted differences in the paper chromatographic pictures from tissues of fish taken not only from different species but also from geographically separated populations of the same species. According to these authors, however, the free amino acids did not play an important role in their results.

The method used in our work and in that of Micks and Ellis (1951) was designed to show the free amino acid constitution (as compared to amino acids "bound" in other molecules) of an entire organism. The methods of preparation of the material were described in some detail in a previous paper (Clark and Ball, 1952). In the present experiments the bodies of approximately forty starved mosquitoes were homogenized; the homogenate was deproteinized with cold ethanol and filtered. After several washings of the precipitate, the resulting filtrate, which contained the amino acids, was reduced to a

usable volume (approximately 100γ) and added in small drops near a corner of 15×15 inch or 6×7 inch sheets of Whatman No. 1 filter paper. The size of the spot containing the concentrate was maintained at 1/16 to 1/8 inch in diameter. The end of the paper nearest to the spot was next immersed in a suitable solvent in a closed jar for approximately eight hours. The paper was then removed and dried at room temperature. The various amino acids move different distances in the solvent and are concentrated in definite positions on the filter paper. If the paper is now turned at right angles to its previous position and exposed to a second and different solvent, migration of the amino acids takes place in a second dimension, thus giving greater separation. If the paper is sprayed with a "developer" solution, the positions taken up by the various amino acids become visible and can be measured on a scale. Identification is made by comparison with tables of the positions of the spots for known amino acids with the solvents used, as well as by running samples of each amino acid and superimposing its spot on the chromatogram of the solution being examined.*

Clark and Ball (1951, 1952) reported on the distribution of free amino acids in the whole bodies of certain culicid mosquitoes and of other insects found in southern California. The culicids studied were *Culex tarsalis, C. stigmatosoma, Aedes varipalpus* and *Culiseta incidens.* The analyses were made by the use of the two-dimensional ascending paper chromatographic technique of Williams and Kirby (1948). Subsequent to the publication of our first report Micks and Ellis (1951), using seven different species of mosquitoes from Texas (*Culex quinquefasciatus, C. pipiens, C. salinarius, Aedes aegypti, A. sollicitans, Anopheles quadrimaculatus,* and *Culiseta inornata*), reported on the presence of 18 amino acids found in the bodies of adult females of all the species tested. They also employed paper chromatographic technique for their determinations. Micks and Ellis, in comparing the paper chromatograms of the three species of *Culex,* namely *C. pipiens, C. quinquefasciatus* and *C. salinarius,* noted the very great similarity between the patterns of the first two species, which are difficult to separate morphologically, and the absence of one amino acid, aspartic acid, in the chromatogram of *C. salinarius.* They also observed a considerably higher concentration of amino acids in *C. quinquefasciatus* and in *Aedes aegypti* as compared to *Anopheles quadrimaculatus.* Micks and Ellis found some amino acids which we did not find in our species at the concentrations used (1951). Subsequently (1952), using heavier concentrations of mosquitoes, we were able to detect most of these with the following exceptions: (1) aspartic acid could not be demonstrated in *C. stigmatosoma* even at a concentration five times that at which it could be shown for *C. tarsalis,* and (2) cysteic acid was present in *C. tarsalis* and in *C. stigmatosoma* although it did not appear in the culicids from Texas.

There are three possible explanations of these different results. They might be due (1) to different techniques, (2) to geographical or ecological factors affecting the biochemical makeup of insects found in different regions, or (3) to actual biochemical differences between species of the same genus.

Since some of the species examined by Micks and Ellis (1951, 1952) occur also in southern California, the opportunity was offered to test the validity of the three hypotheses listed above. We chose *Culex quinquefasciatus,* as it is common in southern California and is the only species found here the amino acid composition of which is described in both the 1951 and the 1952 papers of Micks and Ellis. In order to duplicate their technique more

* For a brief discussion of the theory of paper chromatography and a description of the uses to which it may be put in the laboratory, the reader is referred to *Paper Chromatography, a Laboratory Manual,* by R. J. Block, R. LeStrange, and G. Zweig. 1952. (New York, Academic Press).

closely, amino acid preparations of the specimens of the three species of *Culex* (*C. tarsalis, C. stigmatosoma,* and *C. quinquefasciatus*) were made by deproteinization with 50 per cent ethanol followed by chloroform extraction instead of by evaporation of the filtrate. This was done despite the probability that there would be less loss of material by the latter method (Clark and Ball, 1952). As a further check, amino acid determinations of all three species were carried out according to our original technique, in which the homogenized adult mosquitoes are deproteinized with cold 85 per cent ethanol. The results for the three species are shown in Table I. As far as *C. quinquefasciatus* was concerned there was practically complete agreement with the reports of Micks and Ellis. The only discrepancy concerns aspartic acid, which we were able to detect both in the pupae and in the adults. In their earlier paper, Micks and Ellis (1951) report aspartic acid in adult *C. quinquefasciatus* and so designate a spot on the figure of the chromatogram of this species. However, in the later paper (1952), these authors found aspartic acid only in the eggs and larvae but not in the pupae or adults. In addition, tests were run on *C. quinquefasciatus* adults for hydroxyproline, which was not found, and for α-amino-n-butyric acid and for glutathione, where positive spots were obtained.

From these findings, therefore, it seems evident that the differences in the amino acids reported on the one hand for *Culex quinquefasciatus* by Micks and Ellis (1951, 1952), and on the other for *Culex tarsalis* and for *C. stigmatosoma* by Clark and Ball (1951, 1952), are valid differences and are not based on variations in technique or upon environmental effects due to geographical or ecological isolation. It appears that we have here definite biochemical distinctions among species of a single genus of insects.

In view of these results, it is suggested that paper partition chromatography of amino acids, especially if they are obtained from entire organisms, may offer an additional and useful method of delineating species differences or of indicating phylogenetic relationships. It should be empha-

TABLE I—CHROMATOGRAPHIC ANALYSES OF FREE AMINO ACIDS IN THREE SPECIES OF *CULEX*—SOUTHERN CALIFORNIA

AMINO ACIDS	*C. TARSALIS*	*C. STIGMATOSOMA*	*C. QUINQUEFASCIATUS*
alanine	+	+	+
arginine	+	+	+
aspartic acid	+	−	+
cysteic acid	+	+	−
glutamic acid	+	+	+
glycine	+	+	+
histidine	+	+	+
hydroxyproline	−	−	−
isoleucine and/or leucine	+	+	+
lysine	+	+	+
methionine	+	+	+
phenylalanine	−	−	−
proline	+	+	+
serine	+	+	+
threonine	+	+	+
tryptophane	+	+	+
tyrosine	+	+	+
valine	+	+	+
β-alanine	+	+	+
α-amino-n-butyric acid	+	+	+
asparagine	−	−	−
glutamine	+	+	+
taurine	+	+	+
glutathione	+	+	+

sized, however, that such results are reliable only if the specimens are obtained and treated under identical conditions. Apparent distinctions may in many cases involve different concentrations of the same amino acid instead of the presence or absence of certain specific ones.

Summary

Differences between the free amino acids present in species of *Culex* had been reported by two sets of workers, one from Texas and one from southern California. However, different species had been studied by the two groups, using slightly different techniques. The present chromatographic analysis of *Culex quinquefasciatus* from southern California shows the same amino acid picture as had been reported for this species in Texas. The free amino acids of this species differ from those of *C. tarsalis* and *C. stigmatosoma,* both from southern California, which in turn differ from each other. Identical techniques for the determinations were used throughout. These biochemical differences appear, therefore, to be characteristic of these congeneric species, and cannot be attributed to variations in techniques or to geographic or to ecological factors.

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Points of View

An Animal Census for 1958?

In the course of searches into numbers of insects and other animals (Sabrosky, 1952), the writer was impressed by the assortment of counts, estimates, and guesses that are available, and by the wide interest shown in figures on the number of species of the animal groups. A few of the available figures have been brought together here to illustrate the variety in both total number of species and numbers in the major phyla (Table I).

In some cases, small differences are no doubt the result of varying assignment of minor phyla or groups of uncertain position. For larger groups, however, where it is more difficult to secure reliable statistics, there are considerable differences in the numbers, as in the range of 15,000 to 30,000 for Protozoa, or 40,000 to 104,000 for the Mollusca, or 38,000 to 102,000 for the Chordata. In the Insecta, which includes between 70 and 80 per cent of all known animal species according to most authors, the usual estimates range from 660,000 to 900,000, and both higher and lower figures can be found in the literature. The writer's estimate of 686,000 known species is near the lower limit of the range.

Why could not the Society of Systematic Zoology sponsor a census of the Animal Kingdom, to be completed in 1958, the 200th anniversary of the tenth edition of the *Systema Naturae?* To be sure, the census would be out of date as soon as completed, as are all censuses. But all have their recognized value. What more fitting time than the Linnaean Bicentennial to erect a milestone of reference on the path of man's progress toward a complete knowledge of his animal evironment!

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Table I—Numbers of Species in the Animal Kingdom

Phylum	Hunter & Hunter (1949)	Storer (1951)	Hegner & Stiles (1951)	Stammer (1950)	Ross (1948)	Mayr, Linsley, Usinger (1953)
Protozoa	30,000	30,000	29,000	20,000	15,000	30,000
Porifera	3,000	5,000	5,000	4,500	3,000	4,500
Coelenterata	9,000	10,000	10,000	9,000	5,000	9,000
Platyhelminthes	6,000	7,000	6,500	5,275	6,500	6,000
Nematoda	3,000	6,000	10,000	5,000	3,500	10,000
Annelida	6,000	6,500	7,500	6,690	5,000	7,000
Arthropoda						
Insecta	660,000	675,000	700,000	750,000	900,000	850,000
Others	63,000	65,000	70,000	58,100	50,000	73,315
Mollusca	40,000	45,000	90,000	104,000	80,000	80,000
Echinodermata	4,800	5,000	6,000	4,500	5,000	4,000
Minor phyla	7,300	6,500	—	7,635	4,000	7,025
Chordata	60,900	45,000	102,000	61,600	38,000	39,470
Totals	892,000	906,000	1,036,000	1,036,300*	1,115,000	1,120,310

* Stammer gave the total as 1,025,000.

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Homomorphy

In his recent article on "Regularity of Form in Organisms" Prof. Michael M. Novikoff (1952, p. 60) mentions that he "proposed the term *homomorphism* or *homomorphy*," obviously referring to an earlier paper of his (1935, p. 392). That was, however, not the first time that term was proposed. It was proposed more than half a century earlier by J. A. Palmén (1884, p. 17; for verbal quotation see Haas and Simpson, 1946, p. 329). Novikoff's and Palmén's terms are, thus, obviously homonymous; to judge by the first definitions given by both authors, they seem to be also synonymous, or nearly so.

By way of appendix it should be noted that Novikoff in his last paper as in previous ones uses the term parallelism which to him includes analogy, homology, and homomorphy, with a much more comprehensive meaning than, and quite a different one from, the technical meaning given it in contemporary literature (see Haas and Simpson, 1946, p. 330, 333–339).

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OTTO HAAS
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Editor,
SYSTEMATIC ZOOLOGY:

Recently it has come to the writer's attention that there are several requirements of the International Commission on Zoological Nomenclature with which he was not formerly cognizant. The following excerpts from personal correspondence with Mr. Francis Hemming, Secretary of the International Commission on Zoological Nomenclature, may be of some benefit to others in calling to their attention these requirements.

At the end of January, Henry K. Townes and the writer submitted a paper to the Washington Entomological Society and it was duly accepted for publication. On January 31, 1952, the following letter was sent to Mr. Hemming.

"In the September 28, 1951, *Bulletin of Zoological Nomenclature,* 6, pt. 2:33-64, there is a discussion by Robert Potts on the type of *Geotrupes* (Commission's reference Z.N. (S.) 338).

After reviewing the literature we have come to somewhat different conclusions than Potts and have submitted a manuscript on the subject to the Washington Entomological Society for publication in their *Proceedings.* Since it will not be published for more than a year and would have appeared too late for your consideration (as stated in *Science, 114,* 673, 1951), we are enclosing a copy of the paper herewith."

The following letter was received from Mr. Hemming about March 20, 1952:

"I write to thank you for your letter of 31st January, with which you enclosed for the consideration of the Commission the interesting paper prepared by Dr. Henry Townes and yourself on the above subject. Since, as I have no doubt you know, *matters can be brought before the Commission in relation to cases of this kind only by being published in the Bulletin of Zoological Nomenclature,* [italics mine] I have sent your paper to the printer. [It is here that the requirements

have appeared that had not been known to the writer. First, the necessity of publication in the *Bulletin,* and secondly, publication of a paper without previous permission of the authors. The letter continues:] It is probable that it will be published next month (April). When therefore you later receive proofs from the Washington Entomological Society's *Proceedings,* you will no doubt add a reference to the publication of your paper in the *Bulletin.* If publication takes as long as you say, I should expect that the Commission will have taken its decision before the part of the *Proceedings* containing your paper appears. I mention this, as you may feel that it would hardly be worthwhile publishing this paper a second time and after the matter has been settled."

In reply to this, the authors felt that they should provisionally accept Mr. Hemming's actions and the following reply was made on March 25, 1952:

"We have discussed your proposal concerning the publication of our joint paper on the type species of *Geotrupes.* A copy of the manuscript was submitted in case the Commission was interested in the data contained. We should be glad to have it published promptly in the *Bulletin of Zoological Nomenclature* if we can have 250 separates of the article at a cost of not more than $15.00. [This provision was included as the *Bulletin* is, to say the least, expensive.] The distribution of the *Bulletin of Zoological Nomenclature* is rather limited and we feel the need of the separates to supplement this distribution and to exchange with correspondents. If this number of separates will not be available within the cost indicated *we had rather you not publish the paper* [italics mine]. If lack of publication in your *Bulletin* would preclude consideration by the Commission, we will not be concerned as the record will show that the Commission was not ignorant of the content of the manuscript. Certainly the *Proceedings of the Entomological Society of Washington* would not be interested in publishing articles already printed elsewhere."

There was no acknowledgement of this letter or any other correspondence from Mr. Hemming. The paper appeared in the May issue of the *Bulletin* and the authors to date have received a total of 25 separates. I do not believe there is need for further comment.

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SYSTEMATIC ZOOLOGY is published quarterly by the Society of Systematic Zoology. Its purpose is threefold: To publish, and therefore to encourage the preparation of, contributions on basic aspects of all fields of systematics, principles and problems; to provide a suitable forum for discussion of the problems of the systematist and his methods; and to report as news the other activities of the Society of Systematic Zoology.

Contributions of the following types are solicited: Papers on principles and the applications of principles of wide implication and general interest in any phase of systematics, such as comparative anatomy, zoogeography, paleontology, taxonomy, classification, evolution, or genetics; discussions of methods, specific problems, and activities of systematists; discussions of new books and monographs; and news of systematists, organizations interested in systematics, research and teaching programs, expeditions, collections, meetings, and anything else of interest to systematists.

Major articles should be from 1500 to 10,000 words in length. Discussion articles should not be over 400 words unless of very general interest. Contributors are encouraged to submit line drawings and diagrams to illustrate their articles. Half-tones may be accepted where necessary to the article.

THE PUBLICATION FUND

A Publication Fund was established to help in the initiation of this journal. It consists entirely of donations from the members. It is hoped that it will be a permanent fund for use in other publication programs as well. For this reason further contributions of any amount will be welcomed. At present this fund is restricted to use for SYSTEMATIC ZOOLOGY, under the supervision of the Council.